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SYMPOSIUM ON GEOGRAPHICAL DISTRIBUTION PRESENTED BEFORE A JOINT SESSION OF THE AMERICAN SOCIETY OF ZOOLOGISTS, THE AMERICAN SOCIETY OF NATURALISTS AND THE ECOLOGICAL SOCIETY OF AMERICA*

THE FISHES OF THE PACIFIC SLOPE OF SOUTH AMERICA AND THE BEARING OF THEIR DISTRIBUTION ON THE HISTORY OF THE DEVELOPMENT OF THE TOPOGRAPHY OF PERU, ECUADOR AND WESTERN COLOMBIA[1]

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THE freshwater fish fauna of South America is the richest in the world, both in the actual number of species and the relative number of autochthonous genera and families. All but a few strays and a few species in the extreme southern end of the continent are peculiar to South America.

This fauna developed with the present form and topography of the continent. It is a mistake to assume that the continent, or any part of it, was formed and became planted later. The development of the fauna was and is intimately associated with the development of both the shape and topography of the continent.

* Cambridge meeting, December 29, 1922. The first four papers were printed in the issue of THE AMERICAN NATURALIST for March–April.

[1] Contribution from the Zoological Laboratory of Indiana University. No. 184.

In "The Freshwater Fishes of Patagonia and an Examination of the Archiplata-Archhelenis Theory," [2] I reviewed the knowledge of the distribution of the freshwater fishes of South America and outlined a program for future work. I have been at work on the program outlined ever since—in fact for some time before 1909, the date of publication, for the plan was made several years earlier. An outline for work in Panama and western Colombia was published in 1905 [3] and an abstract of the whole scheme in 1906.[4]

The present paper reviews the work and presents some of the general conclusions reached from the work in Panama, western Colombia and the Pacific slopes of Ecuador, Peru and Chili.

The late Dr. S. E. Meek and S. F. Hildebrand did the field work in Panama. Their volume, "The Fishes of the Fresh Waters of Panama," was published in 1916.[5] (Their volume on the marine fishes is going through the press.)

I travelled in the early part of 1912 from Panama to Cartagena, Colombia, went up the Magdalena and to Bogota, then westward to the coast at Buenaventura. Then I went up the San Juan, crossed the low divide to the Atrato and descended that stream to its mouth.[6] In 1913, Messrs. Arthur Henn and Charles Wilson (The Landon-Fisher Expedition) collected in the Patia in southwestern Colombia and in the lower San Juan. Later Mr. Wilson came over the divide to the Atrato and supplemented my work in that stream while Mr. Henn (The Landon Expedition) went to western Ecuador and examined the Guayas basin and the plateaus of Ecuador.[7]

[2] *Reports of the Princeton University Expeditions to Patagonia*, III, 1909.

[3] *Science*, N. S., XXII, pp. 1–20, July, 1905.

[4] *Popular Science Monthly*, June, 1906, pp. 515–530.

[5] *Field Museum Publications*, Zool. Ser. X, No. 15, pp. 1–63 and 1–252, 1916.

[6] Some results from an ichthyological reconnaissance of Colombia, South America, *Indiana University Studies* No. 16, particularly pages 1–9, Dec., 1912.

[7] "Indiana University Expeditions to Northwestern South America," *Science*, N. S., XL, pp. 602–606, 1914.

In 1918 and 19, during the Irwin Expedition,[8] I examined some of the Pacific slope streams of Peru, and Chili, from Paita, about 5° S. to Puerto Montt at 41° 28′ S.

During the Centennial Expedition of Indiana University[9] Dr. W. R. Allen made additional collections in the Rio Rimac.

Lastly, Mr. N. E. Pearson, a member of the Mulford Expedition, 1921, made collections in the Rio Tambo, southern Peru.

The field work thus covered the Pacific slope of South America from the Panama Canal to Puerto Montt in Chili.

Both in Panama (the Chagres) and Colombia (the Magdalena and Atrato) the work included streams emptying into the Caribbean, *i.e.*, the Atlantic. All of these are, however, west of the Cordillera of Bogota, at present an insuperable barrier to lowland fishes.

ACKNOWLEDGMENTS

I must acknowledge the hearty cooperation of the authorities of Indiana University, and of the Republics of Colombia, Peru and Chili.

The expenses for my "Reconnaissance of Colombia" were met by the sale to the Carnegie Museum of Pittsburgh, Pa., of the first series of fishes and duplicates after a series had been set aside for Indiana University. Messrs. Hugh McK. Landon and Carl Fisher, both of Indianapolis, provided for the expenses of Messrs. Henn and Wilson in Colombia. Mr. Landon and Indiana University provided for Mr. Henn's expenses in Ecuador.

The Irwin Expedition, which collected in Lake Titicaca and on the Atlantic slope, as well as on the Pacific slope, was financed by a grant from the Bache Fund of the National Academy of Sciences, by two grants from the American Association for the Advancement of Science,

[8] *Science*, N. S., L, pp. 100–102, Aug., 1919; *Indiana University Alumni Quarterly*, January, 1920, pp. 1–16.

[9] *Science*, N. S., LIII, pp. 377–379, 1921; *Indiana University Alumni Quarterly*, April, 1921.

by a gift from Mr. William Irwin of Columbus, Indiana, and by appropriations from the Universities of Indiana and Illinois.

The Centennial Expedition of Indiana University also had the cooperation of the Bache Fund of the National Academy of Sciences. Particular thanks are due to the various persons who cooperated with me in the field, Mr. Arthur Bierman, Mr. Arthur Henn, Mr. Charles Wilson, Dr. William Ray Allen, Mr. Nathan Pearson and Dr. Adele Eigenmann (Mrs. John Eiler).

THE NATURE OF THE PACIFIC SLOPE BETWEEN THE PANAMA CANAL AND PUERTO MONTT

Topography.—In the region of the Panama Canal the continental divide is but 9 miles from the Pacific ocean. It is but 8 miles from the old city of Panama to the divide. East of this point it shifts toward the Atlantic. From opposite the Chepo about 79° W. to about 8° 15′ N. and 77° 15′ W. the crest averages about five miles from the Atlantic. At the latter point it turns southwest and from 7° N. to about 5° N. the crest of the coastal Cordilleras, which here forms the divide, varies from a few hundred feet to twenty miles from the Pacific. At 5° N. it suddenly shifts from the coastal to the western Cordilleras of Colombia to include the Rio San Juan basin in the Pacific slope. It runs along the crest of the western Cordilleras to the Rio Patia. This river has cut through the western Cordilleras and has captured some of the upper tributaries of the Rio Cauca of the Atlantic slope. South of the Patia, the Mira, Esmeraldas, Chimbo, Chanchan, Naranja, Romido, Tumbez, and Catamayo have also cut through the crest of the western Cordilleras translating the divide to the eastern Cordilleras. In Ecuador the continental divide runs along the eastern Cordilleras in the north, shifts from the eastern to the western (at 40′ S.) to the eastern again (just south of 2° S.) to the western once more (near 2° 30′) to the eastern once more (3° 20′). From northern Peru it follows the crest of the western Andes

to Chili. In its widest part in Ecuador, near the equator, the slope is 160 miles from crest to ocean, in its narrowest part near 3° S., it is about 30 miles from the ocean. Here the Atlantic slope is one hundred times wider than the Pacific slope. In Peru the slope varies in width from about 50 miles to 150 miles. Between the northern border of Chili to Puerto Montt it varies from 50 to 200 miles in width. The average width between central Colombia and Puerto Montt in a length of over 3,000 miles is less than 100 miles. Between the Panama Canal and Puerto Montt the width varies from a few hundred feet to 200 miles.

The crest everywhere between central Colombia and Valdivia is at present an insurmountable barrier to the intermigration of all but the highest mountain fishes of the genera Orestias, Pygidium and Astroblepus. To the most of the species of even these genera the transmigration of the Andes has been and is impossible.

Strategic points in the continental divide are: (1) Culebra between the Chagres and the Pacific slope streams with a height of about 334 feet. (2) Cajal pass in eastern Panama, between the Tuyra of the Pacific and the Atrato of the Atlantic, with a height of about 400 feet. (3) The Istmina pass between the Atrato of the Atlantic and the San Juan of the Pacific with a height of about 300 feet. (4) The Patia, which has robbed the Cauca of the Atlantic slope. South of the Patia the continental divide is mostly over 9,000 and 10,000 feet, except inland from Piura where a saddle reaches an elevation of but about 7,000 feet. Just south of 40° S. in Chili the headwaters of the Calle Calle arise east of the main crest of the Andes. Near Puerto Montt a pass between the Petrohué Basin and the Nahuel Huapi Basin is but 3,000 feet high, and south of this point rivers of one side not infrequently have their origin on the other side of the main crest. The story of the shifting of the continental divide in Ecuador is repeated in southern Chili, but now at much lower altitudes.

Moisture.—The rainfall in different parts of the slope varies from nearly 400 inches per annum to nothing. In Panama, Colombia and northern Ecuador, the rainfall of the Pacific slope is excessive. In Piura, northern Peru, it rains once in many years. When at Piura I asked, "Where is the river?" I was told, "It has not come down yet; we expect it next Saturday." In the north the mountains cast rain shadows eastward. Southward the mountains cast rain shadows westward.

Southward of Guayaquil the rivers become more and more uncertain to northern Chili where only the mountain-fed Loa crosses the arid slope. South of the desert of Atacama rivers are again found occasionally. The first of them is the Rio Copiapo. Between La Serena and Vallenar, I was told that after a rain all the hills became covered with flowers. When I asked about the rainy season I was informed that it had rained once in those parts about eleven years before. In this arid region of Chili there are great valleys from crest to ocean but the rivers that made them are extinct and so naturally are the fishes that inhabited them.

South of Valparaiso valleys are also abundant and water becomes more and more abundant. The region between Concepcion with its Rio Bio Bio and Puerto Montt is supplied with numerous lakes and rivers. The rainfall in this region is again very great, but not so great as in Panama and Colombia. The region from Panama to the boundary of Chili lies in the tropics, the climate north of Guayaquil is tropical but south of Guayaquil temperate. The rivers of Chili between the Copiapo and Puerto Montt all lie in the south temperate region.

THE NATURE, ORIGIN AND DISPERSAL OF THE FISHES

I have dealt with the details of the fishes of the Pacific slope of South America in a series of papers[10] published in various places.

[10] 1. "Some Results from an Ichthyological Reconnaissance of Colombia, South America," *Indiana University Studies*, No. 16, Sept., 1912. (Issued December 23.)

There remains scarcely a doubt about the origin of any of the present genera of the entire Pacific slope. (Footnote 10, no. 14.)

2. "Some Results, etc.," Part II, *l. c.*, No. 18, March, 1913. (Issued in June.)
3. "New Fishes from Western Colombia, Ecuador and Peru" (in collaboration with Arthur Henn and Charles Wilson), *l. c.*, No. 19, January, 1914.
4. "Some Results from Studies of South American Fishes," *l. c.*, No. 20, March, 1914. (Issued in April.)
5. "On New Species of Fishes from the Rio Meta Basin of Eastern Colombia and on Albino or Blind Fishes from near Bogota," *l. c.*, No. 23, September, 1914.
6. "On New Species of Fishes from Colombia, Ecuador and Brazil" (in collaboration with Arthur Henn), *l. c.*, No. 24, September, 1914.
7. "The Gymnotidæ of Trans-Andean Colombia and Ecuador," *l. c.*, 25, September, 1914.
8. "South America West of the Maracaibo, Orinoco, Amazon, and Titicaca Basins and the Horizontal Distribution of its Fresh-water Fishes," *l. c.*, No. 46, pp. 1–19, map, September, 1920. (Issued January, 1921.)
9. "The Fishes of the Rivers Draining the Western Slope of the Cordillera Occidental of Colombia, Rios Atrato, San Juan, Dagua, and Patia," *l. c.*, No. 46, pp. 1–19, map, September, 1920. (Issued January, 1921.)
10. *A.* "The Fresh-water Fishes of Panama East of Longitude 80° W." *B.* "The Magdalena Basin and the Horizontal and Vertical Distribution of Its Fishes," *l. c.*, No. 47, pp. 1–34, maps, December, 1920. (Issued May, 1921.)
11. "The Fish Fauna of the Cordillera of Bogota," *Journ. Washington Acad. Sci.*, X, pp. 460–468, Oct., 1920.
12. "Eighteen New Species of Fishes from Northwestern South America," *Proc. Am. Philos. Soc.*, LVI, pp. 673–689, 1917.
13. "Description of Sixteen New Species of Pygidiidæ," *l. c.*, LVI, pp. 690–703, 1917.
14. "The Origin and Distribution of the Genera of the Fishes of South America West of the Maracaibo, Orinoco, Amazon and Titicaca Basins," *l. c.*, LX, pp. 1–6, 1921.
15. "The Nature and Origin of the Fishes of the Pacific Slope of Ecuador, Peru and Chili," *l. c.*, —, pp. —, 1921.
16. "The Cheirodontinæ, a Subfamily of Minute Characid Fishes of South America," *Mem. Carnegie Mus.*, VII, pp. 1–99, 36 text figures, plates I–XVII.
17. "*Pimelodella* and *Typhlobagrus*," *l. c.*, VII, pp. 229–258, plates XXIX–XXXV, 1917.
18. "The Pygidiidæ, a Family of South American Catfishes," *l. c.*, VII, pp. 259–398, 39 text figures, plates XXXVI–LVI, 1918.
19. "The Fishes of Western South America, Part I. The Fresh-Water Fishes of Northwestern South America, including Colombia, Panama, and the Pacific Slopes of Ecuador and Peru, together with an Appendix upon the Fishes of the Rio Meta in Colombia." *Mem.*

On the Pacific slope between Panama and southern Chili there are two main faunas. That of Chili belonging to the south temperate Patagonian fauna is flavored with but a suspicion of the tropics. It is poor in species, there being but 35 known species in all the rivers of Chili north of Puerto Montt.

The fishes of the rivers north of Lima pertain to the tropical fauna of the Amazon-Orinoco and Central America with but a few occasional north temperate surprises. Three hundred and eighty-five species have been taken in the rivers of Colombia west of the Cordillera of Bogota and on the Pacific slopes of Ecuador and Peru. This area is divisible into several distinct regions.

The highland fauna (above 7,000 feet) in part overlaps the different lowland faunas.

THE FAUNA OF CHILI

The fauna of Chili, consisting of but thirty-odd species, is completely distinct from that north of Lima, Peru. A very large per cent. of it has immigrated from the ocean, a smaller part came from the north, another small part is autochthonous.

Carnegie Mus., IX, 1922 (issued January, 1923), pp. 1–346, text figures, plates I–XXXVIII.

20. "On *Apareiodon*, a New Genus of Characid Fishes," *Ann. Carnegie Mus.*, X, pp. 71–76, plates XI–XII, 1916.
21. "New and Rare Fishes from South America," *l. c.*, X, pp. 77–86. Text figures 3, plates XIII–XVI, 1916.
22. "Description of Three New Species of Characid Fishes" (in collaboration with Arthur Henn), *l. c.*, X, pp. 87–90, plate XVII, 1916.
23. "On the Species of *Salminus*," *l. c.*, X, pp. 91–92, 1916.
24. "On Various South American Pœciliid Fishes," by Arthur Henn, *l. c.*, X, pp. 93–142, plates XVIII–XXI, 1916.
25. Report as Curator of Fishes in Carnegie Museum. Seventeenth Ann. Rept. of the Director, 1914, pp. 19–22.
26. "The Freshwater Fishes of Chili," nearly completed.
27. "Yellow Fever and Fishes," *Proceedings American Philosophical Society*, LXI, 1922, pp. 204–211.
28. "A Catalogue of the Freshwater Fishes of South America," *Proc. U. S. Nat. Mus.*, XIV, 1891, pp. 1–81. Aside from listing the species this paper discusses various phases of the distribution of genera, including those of the Pacific slope.

Part of the oceanic contribution came from the south and is common to Australia, New Zealand, Patagonia and Chili. The point of origin of this element of the fauna is in doubt, unless there was a habitable antarctic continent in which the Galaxiidæ, Aplochitonidæ and Lampreys developed and from which they moved north in all directions. In Chili this part of the fauna moved from its point of origin to different points north, some of the lampreys to Valparaiso, *Galaxias maculatus* and Aplochiton to Concepcion, other fishes apparently only to Valdivia, the northernmost point where the Lampreys, the Galaxiidæ, and the Aplochitonidæ are still at their best. The species are abundant in the streams having lakes in their headwaters.

The other oceanic contribution to the freshwater fauna came from the temperate sea. (*a*) The genus Cauque of the Atherinidæ is but little different from Austromenidia, at the present time abundant on the coast of Peru and Chili. Cauque occurs from La Serena southward (on both slopes). (*b*) The genus Basilichthys, also of the Atherinidæ, is of older standing, ranging in the rivers at least from Lima to Puerto Montt. In this range three species have become differentiated, one in Peru, one in Chili north of Santiago, and one south of Santiago. (*c*) The genus Percichthys, confined to Chili and Patagonia, from Punta Arenas as far north as there is suitable water (Rio Aconcagua) is a thoroughly freshwater genus belonging to the marine family of the Serranidæ. It is an ancient contribution from the sea. (*d*) The genus Percilia, also of the Serranidæ, probably has a similar history.

The contribution from the north consists of (*a*) Pygidium, a mountain catfish found in all the mountains of South America, (*b*) Hatcheria, a Patagonian modification of Pygidium, (*c*) Cheirodon, a minute characin ranging from Panama south (see no. 16, footnote 10), is the only contribution from the tropical fauna of South America. The presence of Cheirodon in Chili probably dates back to the time when Argentina was a suitable

habitat for the genus as far south as the great lakes of Patagonia. It has retained its primitive structure in and near the Bio Bio basin. Less typical species have developed north and south of the Bio Bio region.

The third, the autochthonous element of the fauna, is the most ancient. It consists of but two species, *Nematogenys inermis* and *Diplomyste Chilensis*. (*a*) Diplomyste is found between Santiago and Buenos Aires on the north, and Valdivia on the south. It is autochthonous, one of the original Patagonians, a catfish in which the maxillary still carries teeth. (*b*) The last of the Chilian fishes is *Nematoyenys inermis*, confined to central Chili. It is the most primitive or generalized member of the Pygidiidæ, lacking some of the most characteristic features of the family, differing in fact so much that it might well be considered the type of a distinct family, the Nematogenyidæ. This genus is also autochthonous, the first, original "Chileno."

Chili is divisible into the following regions:

a. The "Austro-Chilian" extends north to Valdivia and is characterized by the abundance of Lampreys, Galaxias, and Aplochiton and the absence of Nematogenys. It is the region of the great lakes.

b. The "Intermediate" between Valdivia and Concepcion is characterized by the waning of the Galaxiidæ and Aplochitonidæ.

c. The "Chilian" from Concepcion to Santiago is characterized by Nematogenys, Diplomyste and the absence of Galaxiidæ and Aplochitonidæ.

d. The "Region of Relicts" north of Valparaiso. The rivers are small and many have gone dry altogether. Only Cauque, Basilichthys, Cheirodon and Pygidium have been taken north of the Rio Aconcagua; in Choapa only Basilichthys; in Vallenar only Cheirodon; in the Rio Camarones only Basilichthys. Basilichthys will probably be found in all the rivers of the dry region between Lima and Valparaiso that retain any encouragement for the continued existence of fishes.

The freshwater fishes of Chili and Patagonia are so limited in numbers and show such affinity with the marine fauna that I adhere to an opinion I expressed long ago. During the subsidence from which Chili and southern Patagonia are at present rising all the freshwater fishes except those adjusted to also live in the ocean were exterminated. There has not been time or opportunity since its reelevation to impart a new extensive purely freshwater fauna. In the north of Chili and Patagonia during the subsidence there were opportunities for the continued existence of Cheirodon, Pygidium, Nematogenys, Diplomyste and possibly Percichthys and Percilia.

The rate of elevation as measured on rocks outside of Coquimbo is about 25 feet in 200 years.

The Fauna of Western Ecuador and Peru
(See Nos. 15 and 19, footnote 10)

The fauna of the Guayas in Ecuador was derived from the Amazonian fauna. It has less affinity to that of the Magdalena to the north of it than to that of the Amazon east of it. Its origin can best be explained on the assumption that at a time much earlier than the era of the continuity of the Magdalena fauna with that of the Orinoco there was a continuous fish fauna from the Pacific shores of Ecuador and northern Peru to the Atlantic shores. The development of the western Andes of Ecuador and northern Peru isolated the species living west of them from those living east of them. This isolation took place much earlier than the isolation of the Magdalena fauna by the Cordillera of Bogota. It took place before the development of the present species of Ecuador and before the development of many of the genera of the Guayas. Only one species of western Ecuador is also (possibly) found east of the Andes. Twenty-five per cent. of the genera of Ecuador are peculiar. South of Guayaquil, with the elevation of the Andes the genera and species have become exterminated

one after another. The Peruvian rivers draining into the Pacific have at present torrential courses and great seasonal fluctuation which few species of the original fish-fauna have been able to withstand.

The Guayas fauna and the Chilian fauna touch in the Rio Rimac of central Peru where *Basilichthys semotilus* gives the first hint of the Chilian fish-fauna, *Bryconamericus peruanus* and *Lebiasina bimaculata* are all that recall the Guayas. The present Guayas river is probably much younger than the fish-fauna it contains. In the early Quaternary it became the most favorable habitat for freshwater fishes on the Pacific slope and became the gathering place of the entire Pacific slope fauna of southern Ecuador and Peru. It is well separated from the north. Not more than four of its known species are also found north of it.

THE FAUNA OF WESTERN COLOMBIA

(See Nos. 8, 9, 10, 11, 15 and 19, footnote 10)

The fishes of the Pacific slope of Colombia came in very large part from the Magdalena and Atrato basins. The Atrato fishes themselves came in large part from the Magdalena. While the Magdalena and Atrato are not Pacific slope streams, since they are west of an insuperable barrier and have contributed so much to the Pacific slope an examination at this point of the origin of the Magdalena fauna is warranted.

The nature of the Pacific slope and Magdalena fauna can best be explained by the following facts and assumptions: As in Ecuador the oldest of the mountain chains of Colombia is the Cordillera Occidental extending from the hills at Cartagena south to Cape Horn. The formation of this chain with the development of the rivers draining its slopes divided the primitive fauna of Colombia into a western and eastern as it did in Peru and Ecuador. The rivers of the western slope draining into the Pacific were short and the fauna was from the start more limited than the fauna of the much larger Atlantic slopes. In part the fishes of this early segregation were

generically at least identical with those of western Ecuador and Peru. Others were peculiar.

As in Ecuador, the formation of this, the western, chain antedates the present species and many of the present genera. (See No. 9, footnote 10.)

The central Cordilleras of Colombia were the second of the Andean chains to develop. Their development formed the groove in which developed the upper Rio Cauca, the oldest of the larger rivers of western Colombia. If there has been a continuity of the fishes from that day to this, we should get an inkling of the old fauna in the twenty-nine species of fishes taken in the upper Cauca. The western Cordilleras, although in places but 6,000 feet high, have been an effective barrier to the migration of the present fishes of the upper Cauca to the rivers on the Pacific slope. (For details see Nos. 9 and 10, B, of the bibliography in footnote 10.)

The third of the mountain chains to develop are the Cordilleras of Perija and of Bogota. They segregated the Magdalena valley with its fishes from Lake Maracaibo and the Orinoco. The territory segregated by this uplift is much more extensive than that by former mountain formations. It resulted in the development of the Rio Magdalena.

The isolation of the Magdalena basin took place during the lifetime of most of the present dominant genera and during the life of many of the present species. Thirty-four of the species of the Magdalena have retained their specific characters since before the development of the Cordillera of Bogota divided their range. The stripes on the catfish, Pseudolatystoma, which is found on both slopes, are older than these mountains. (See No. 10, B, footnote 10.)

Before the elevation of the Cordilleras of Bogota began to form an effective barrier to the migration of freshwater fishes the area at present occupied by the Magdalena basin was inhabited, in common with the area to the east of the present Cordilleras of Bogota and

Perija, by a fish-fauna in many respects similar to the present fauna of eastern tropical South America at an elevation of five hundred to a thousand feet. The fishes belong to seventy odd genera. Of the latter the tarpon and eel were contributed by the north via the sea. Eight genera were contributed by Central America, five belong to the high Andes, over fifty are also found east of the Cordillera of Bogota, the rest are evident modifications of eastern genera.

As stated the Cordillera Occidental is the oldest mountain chain in Colombia. Its Pacific slope from the divide to the Atrato and San Juan in the north and the ocean in the south is narrow. Its development segregated a very limited part of the original fauna. The coastal Cordillera to the west of it is the youngest of the mountain chains in Colombia. Its development and denudation in late Tertiary (or Quaternary as Hettner suggests) caused the formation of the Atrato and San Juan rivers in the trough between the western and coastal Cordilleras. They gathered the waters of the small streams flowing originally direct from the Cordillera Occidental to the sea, the San Juan carrying the water of those south of Istmina into the Pacific, the Atrato carrying the waters of those north of Istmina into the Atlantic. The development of the large Atrato river provided a suitable environment for many of the fishes which had not found an environment in the small mountain torrents. Some of the fishes of the Magdalena migrating westward along the low coastal plain (via the Sinu?) and around the northern end of the western Cordilleras colonized the new environment provided by the Atrato. Some of the species that got into the Atrato went further, crossing the pass of Cajal into the Tuyra basin, others crossing the pass at Istmina into the San Juan basin. Some species that succeeded in crossing the divide at Cajal have not succeeded in crossing the pass at Istmina. Prochilodus and Leporinus have not succeeded in crossing either although

there is favorable environment across both divides (see No. 9, footnote 10) and both genera are also found in Ecuador.

Over 60 per cent. of the known species of fishes of the Atrato came from the Magdalena or have diverged but slightly from Magdalena species.

Of forty-five species migrating westward from the Magdalena into the Atrato, twenty stopped in the Atrato, nine became but slightly modified, eleven got across the divide southward into the San Juan, three more got as far as the Dagua, and five more reached the Rio Patia. (See No. 9, footnote 10.)

The migration into the Atrato, Tuyra, Chepo and southward to the San Juan, Dagua, Patia took place much more recently than the isolation of the Magdalena from the Orinoco if the per cent. of identical species may be taken as a measure of time. The migration probably began before the Magdalena became entirely isolated from the east. About twenty per cent. of the Magdalena species still live east of the Cordilleras of Bogota. The per cent. of species of the western rivers still living in the Magdalena is much greater. Over sixty per cent. of the known Atrato species still live in the Magdalena basin or have representatives there. (There certainly are more.) Thirty-six per cent. of the San Juan species live in the Atrato. Sixty-five per cent. of the Patia (near the boundary of Ecuador) species live in the San Juan, Dagua, Atrato or Magdalena.

These per cents. of identical species in neighboring rivers give an inverse ratio of the length of time the rivers have been separated or of the difficulties for fishes to pass from one to the other.

The Origin of the Panama Fauna

The present fish-fauna of the Isthmus of Panama appears quite recent. The ancestors of the fishes of the Chagres river came in largest part from the south, in much smaller part from the north. The balance came from the ocean.

At least nineteen species have succeeded in crossing the Pass at Cajal, from the Atrato westward into the Tuyra. Others have crossed but have become modified in the Tuyra. Of these species which went from the Atrato to the Tuyra, eleven reached the Chepo and of these eleven, five recrossed the continental divide into the Chagres. (See No. 10A, footnote 10.) The fresh-water fishes of the Atrato have not been able to reach the Chagres by way of the sea. Thirty-eight per cent. of the Tuyra fishes live in the Atrato, thirty-one and five tenths per cent. of the Chepo fishes live also in the Tuyra; seventy-three per cent. of the fishes in the streams opposite the Chagres live also in the neighboring Chepo. Forty-two per cent. of the Chagres fishes live also in the Chepo or the Pacific slope streams opposite the Chagres. The similarities pointed out in this paragraph are for the most part the results of active migrations *since* the development of the Atrato.

The Chagres has received a large per cent. of its fishes from the Atrato via the Tuyra and Chepo. Only one of the Chagres fishes coming from the south (Atrato) has reached as far north as Costa Rica.

The Chagres has received a number of its species from the north. Of these a gar pike has come the farthest. It was recorded long ago but was not found in recent explorations. The common eel occasionally drifts into Panama. The genera Agonostoma, Jotarus and a number of Cichlids are Central American and find their farthest south in or near Panama.

Judging by the present fauna the present isthmus of Panama has not been used as a highway for the intermigration of northern and southern faunas. It is the present meeting place of a stream coming from the south and another coming from the north. (No. 10, footnote 10.)

General Items on the Pacific Slope of Ecuador and Western Colombia

(See No. 19, footnote 10)

1. Certain of the generic types have undergone a very active evolution in this region, giving rise to many species; such are (1) Astyanax (14 species), (2) Bryconamericus (10 species), (3) Creagrutus (6 species), (4) Brycon (13 species), (5) Pimelodella (6 species), (6) Astroblepus (18 species), (7) Pygidium (22 species), (8) Chætostomus (6 species), (9) Loricaria (10 species), (10) Curimatus (8 species), (11) Hemibrycon (7 species), (12) Rœboides (7 species). The second and fourth of these genera have reached their optimum west of the Andes. All of these genera, except possibly 6, antedate the formation of the Andes.

2. Other genera are at present forming incipient new species. Such are Argopleura, Rœboides and Gephyrocharax.

3. The Glandulocaudinæ reach their highest development in western Colombia and in southeastern Brazil and Uruguay. (See No. 4, footnote 10.)

4. The highland fauna. (See Nos. 9, 10B, and 11, footnote 10.)

The highest altitudes are inhabited principally by species belonging to three genera: Pygidium, Astroblepus and Orestias. They are indifferently found both on the Atlantic and Pacific slopes. Astroblepus is found in all suitable places in the Andes from Panama to Lake Titicaca.[11] In Colombia it attains the highest altitude inhabited by fishes but descends in favorable places to 300 feet.

The species of Pygidium are found in all the mountains of South America; on the Pacific slope, all the way from Panama to Patagonia, from 14,000 feet to sea level.[12]

[11] But one species has been found in the Titicaca basin.

[12] The Pygidiidæ have become of unsurpassed economic interest since the discovery by Dr. H. Hanson, of the Rockefeller Foundation, that one of the species of Pygidium (probably all of them) is of supreme importance

Orestias is confined to quiet water above 7,000 feet in Peru and northern Chili. It reaches its optimum in Lake Titicaca.

Pygidium and Astroblepus are mountain scalers, at their best in rapids. Orestias, on the contrary, belongs in quiet water. It could not have ascended to its present height by way of the present torrents. It went up with the Andes. One species of Orestias lives in Death Valley, between California and Nevada.

These three mountain genera to which should probably be added some of the species of Hemibrycon, a Characid and some of the species of Chætostomus, a mailed catfish, belong to an ecological group and obey laws of distribution quite different from those of the lower slopes of the Andes.

THE GEOGRAPHICAL DISTRIBUTION OF THE ONYCOPHORA

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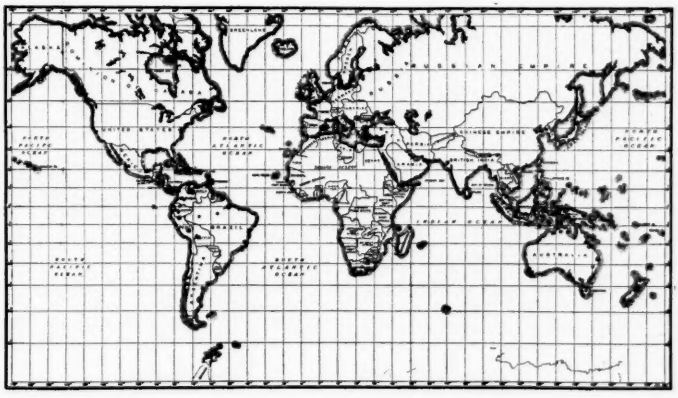
THE Onycophora, familiarly known among zoologists as "Peripatus," now include about eighty species, grouped into more than a dozen genera that form two families. Although they have been thus subjected to the most minute classificatory dissection (Fig. 1) at the hands of the taxonomists, they remain to-day as isolated from any other group of animals as they appeared to be when Guilding, nearly a century ago, described *Peripatus juliformis* as an aberrant mollusc. That the group is now conceded to be more or less transitional between the Annelids and Arthropods is of no moment in the present connection, and we may be content with the statement, which can be made without reserve, that the Onycophora include a number of very closely related species, entirely different from any other animals, widely scattered throughout the tropics of both hemispheres.

in the eradication of yellow fever mosquito larvæ from the storage vessels for drinking water. See footnote 10, Nos. 18 and 27.

The oldest, and indeed the only known, fossil member of the group, *Aysheaia pedunculata* Walcott, has been found in the middle Cambrian rocks of North America; it does not seem to be remarkably unlike the living forms.



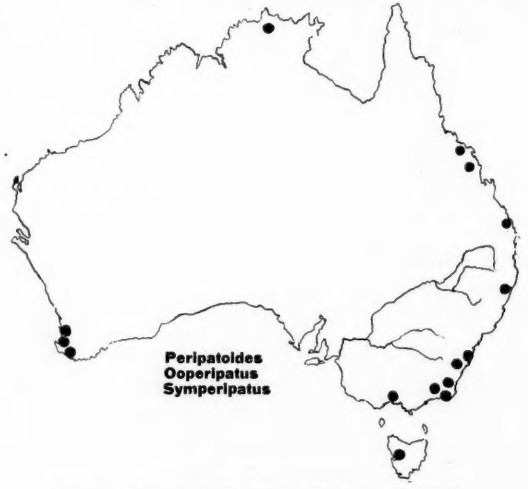
MAP I. World Distribution of Onycophora.

The Onycophora are of interest to the zoogeographer for several other reasons. They are soft-bodied, usually very delicate and sensitive creatures, of secretive habits, and restricted to very specialized habitats. They have thus, undoubtedly, found it very difficult to perform extensive migrations. Also, they are absolutely unfitted for transport by the elements, by rafts, or through the agency of other animals, due to their inability to survive for any length of time under adverse conditions. Similarly the eggs are delicate, and are never even laid by the females of many species, which have become viviparous and produce large living young. We see, therefore, that the present wide and discontinuous distribution of the group is of considerable interest. From Map I, it will be seen that the group occurs mainly in tropical America, South Africa, Australia, New Zealand, Malaya and Indo-China. As the species are often extremely

local and erratic in their occurrence, it is unwise to lay great stress on the apparent absence of Onycophora from any area, but it is quite certain that the group is best represented in the tropical regions just mentioned, and that it is practically absent from the more temperate regions. Thus far no species are known from the Malagasy or Indian subregions and there is only one form recorded from equatorial Africa.

The most primitive family, the Peripatopsidæ, is restricted almost exclusively to the Old World, although one genus, Metaperipatus, occurs in Chile. The Peripatidæ occur in both hemispheres, the two genera of Eoperipatinæ in the Old World and the entire subfamily Peripatinæ in the New World, with the exception of the tropical African Mesoperipatus.

In Australia, including New Zealand and Tasmania (Map II), are three genera, Peripatoides, Ooperipatus

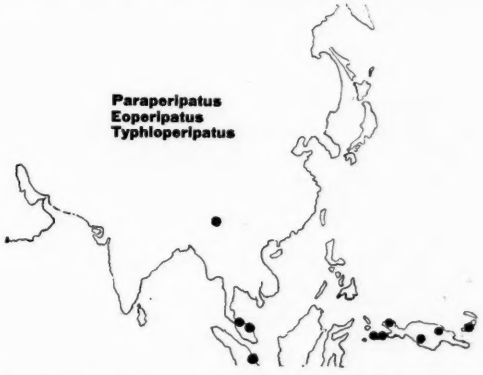


Map II. Distribution of Onycophora in Australia.

and Symperipatus, sometimes included in a single genus and showing the close faunal relationship of Australia and New Zealand.

In the region to the north (Map III) we find three

genera, none of which occurs in Australia. Paraperipatus extends from New Britain through New Guinea into Ceram, but not further; to the west it is replaced by Eoperipatus known from Sumatra and the Malay pen-

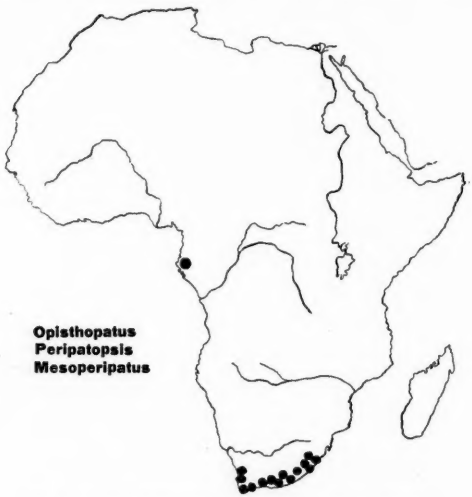


MAP III. Distribution of Onycophora in Asia and the East Indies.

insula. Typhloperipatus further to the north is a rather peculiar type, probably most closely related to Eoperipatus. Thus, in this much discussed Indo-Australian region we find "Wallace's line" separating the Peripatopsinæ and Eoperipatinæ.

In Africa (Map IV) we find three peculiar genera. In Cape Colony, Opisthopatus and Peripatopsis occur together and in apparently complete isolation from other genera. Likewise, Mesoperipatus is the only occupant of the equatorial belt. The single Opisthopatus is related to the Australian Peripatoides and also to a South American genus Metaperipatus, indicating migration probably from Australia to South Africa and thence to America, or possibly first to South America. On the other hand, the second South African genus, Peripatopsis, shows a close relationship to the Ceramese and Papuan Paraperipatus, indicating that there has at some time been an opportunity for migration between these two regions. The African Mesoperipatus is the only member of the Peripatinæ known from the Old World. It has been reported only from the French Congo. This

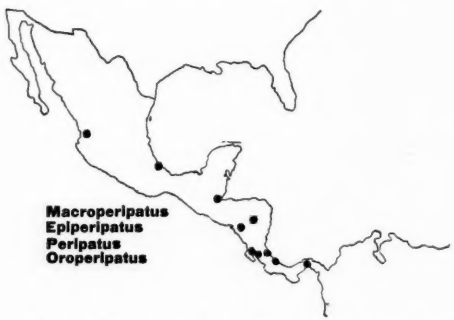
genus combines certain antomical characters of two neotropical types in addition to some peculiarities of its own. From this we may surmise that it has been de-



MAP IV. Distribution of Onycophora in Africa.

rived from some ancient neotropical immigrant that reached Africa from some portion of the South American continent.

The Onycophora are, as we have already indicated, well represented in tropical America, ranging from well up in Mexico at Tepic to south-central Chile (Maps V,



MAP V. Distribution of Onycophora in Central America.

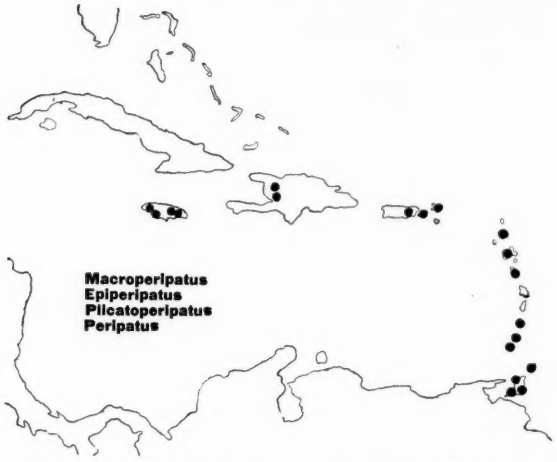
VI, VII). Omitting a single discordant element, represented by the Chilian Metaperipatus, all are quite similar and form the subfamily Peripatinæ, typical of the New World and restricted to it, except for the African

MAP VI. Distribution of Onycophora in South America.

Mesoperipatus, already mentioned. Metaperipatus is referable to the Peripatoidinæ and finds its closest affinities among the African and Australian genera of that group, furnishing another example of faunal relationship between these three areas.

The remaining truly American Peripatinæ fall into five types, all of which I have indicated for convenience on the taxonomic chart (Fig. 1) as genera. They are of unequal value and none are so closely set off as the genera we have previously discussed. More than half of the known species fall into this series, so that considering their similarity and the difficulty in distinguishing many of the species, it is evident that America is at present the seat of a quite active evolution and differentiation of onycophorous genera, species and subspecies. In the Andean Cordilleras and along the Pa-

cific coast are a number of species of Oroperipatus. Some ascend to quite high altitudes in Ecuador and



MAP VII. Distribution of Onycophora in West Indies.

Bolivia, while others occur at sea-level, thus showing a very considerable tolerance to the variable climatic factors of temperature and humidity. Epiperipatus occupies the low-lying, moist, forested areas of the Spanish Main from whence it extends up the Amazon valley, northwards into Guatemala and along the Lesser Antilles to Grenada. Northward from Grenada its place is taken by Peripatus (*sensu stricto*) which has been found in the higher, humid parts of every one of the islands of any size from Carricau to Jamaica, except Martinique and St. Lucia. Strangely enough, however, Cuba has so far yielded no examples and is apparently lacking in Onycophora. Peripatus (*sensu stricto*) occurs also along the Caribbean coast from Costa Rica to Venezuela, thus more or less encircling the Caribbean. As all the species of this group are viviparous and perhaps the most delicate of all Onycophora, they must undoubtedly have reached all the islands over land bridges, or if we object to this term, *via terra firma*. Their absence from

the adjoining islands of Martinique and St. Lucia in the middle of the series may be apparent only. If real, it may probably be traced to extinction through volcanic activity, since as we have already seen, the Antillean species are very delicately adjusted with reference to

FIG. 1. Taxonomic grouping of the genera of Onycophora.

moisture. One other point of interest in connection with the Lesser Antilles is the occurrence of a continental type, Macroperipatus, on Trinidad, beyond which it does not go, although the continental affinities of Tobago and Grenada just to the north are vouchsafed by the extension of Epiperipatus into these islands.

Finally we must not fail to mention a striking type, Plicatoperipatus, represented by a single species, peculiar to Jamaica, lying geographically at the extreme western end of the series of Antillean stations so far reported for Onycophora.

THE GEOGRAPHICAL DISTRIBUTION OF INSECTS AND THE AGE AND AREA HYPOTHESIS OF DR. J. C. WILLIS

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THE English botanist, Dr. John Christopher Willis, some time Director of the Botanical Gardens at Rio de Janeiro, has for the last twenty years devoted much attention to the study of geographical distribution and dispersal of plants. His conclusions have appeared in a number of papers from 1906 on and they have now been gathered up into a volume entitled, "Age and Area, a Study in Geographical Distribution and Origin of Species" (Cambridge, University Press, 1922). The main idea running through this book is what he terms the "rule of Age and Area," stated in his own words as follows:

> The area occupied at any given time, in any given country, by any group of allied species at least ten in number, depends chiefly, so long as conditions remain reasonably constant, upon the ages of the species of that group in that country, but may be enormously modified by the presence of barriers such as seas, rivers, mountains, changes of climate from one region to the next, or other ecological boundaries, and the like, also by the action of man and by other causes (p. 63).

In another place in the same volume, it is stated thus:

> As already several times explained, the general meaning of Age and Area is simply that on averages and in the long run species and genera spread at a more or less uniform rate, interfered with by barriers physical or ecological. On the older view it was imagined that distribution was so rapid that all forms had already reached their limits and that many were in process of contracting their area of dispersal (p. 189, footnote).

In their early stages of growth, Dr. Willis's views were largely derived from a study of the flora of the Island of Ceylon. Some of the species of this island are

confined to it, others are found in Ceylon and in the Peninsula of India but not farther, still others, called for convenience sake the "wides," are found in Ceylon, Peninsular India and in more distant countries. This last class, or "wides," he believes to be the oldest of the three, the second class to be next in age and the first, or species endemic to Ceylon, to be the youngest. Just because they are the youngest they are confined to Ceylon, or even to limited parts of the island, since they have not had time to spread farther. He goes on to explain:

> It is clear, of course, that age in itself can effect nothing, but it allows time for the various factors that are active in distribution to produce their effects. . . . Dispersal therefore becomes a measure of age, except in so far as barriers, physical or ecological, interfere. Distribution is very slow, and probably the vast majority of species have not yet reached the limits that they might reach, if sufficient time were allowed (p. 61).

Some of the conclusions which Dr. Willis reaches with respect to the distribution of living things, both plants and animals, are as follows:

Those species which are most widely distributed in a country are those which have the widest distribution outside thereof while the local or endemic species show the smallest areas of distribution (p. 8).

Endemic species in all regions of the world belong in greater proportion not to the small and local genera but to the large and widespread (p. 165).

The species of endemic genera show less dispersal in a country than the endemic species of non-endemic genera (p. 166).

Distribution of genera within families or of species within genera, whether endemic or "wide," in any given area form "hollow curves," or curves with the mode at one end. This mode corresponds to the maximum number of genera within some larger taxonomic unit, but each genus containing only a single species (monotypic genera). From the mode the curve falls steeply and

then gently declines to the minimum number of genera, but each (or the single) genus has the maximum number of species. The mode of maximum number of genera corresponds also to the smallest area of distribution, while the other end of the curve corresponds to the largest area (p. 166, combination of nos. 6, 7 and 10).

Curves of this nature have been drawn by Dr. Willis for many groups of plants, of various floras, and for some groups of animals and samples are given on p. 237. The numbers for such a curve of the Tenebrionid beetles, taken from Gebien, in the *Catalogus Coleopterorum* of 1910–11, are given as 489 genera of 1 species each, 154 of 2 species each, 103 of 3, 73 of 4, 40/5, 48/6, 32/7, 32/8, 24/9, 10/10 and so on (p. 203).

"Within any circle of affinity, the larger genera will be the older, and when taken in groups of ten allied genera will be older in rough proportion to their numbers of species" (p. 107). While this book says little of the actual ages of the taxonomic units discussed, we are told that the ages are to be "deduced from phyletic, morphological and geological considerations" (p. 108).

The main object of the present paper is to consider the possible application of these conclusions to certain insects.

At the outset, it must be premised that the data on the distribution of insects are not as definite or complete as in the case of plants. This condition is due to insects' powers of locomotion, both as favoring their wider distribution as well as eluding the collector; to the smallness of size of many of the species; and to their concealment on, under or within a great variety of objects.

The dragonfly,[1] or Odonate, fauna of New Jersey embraces 123 species of 44 genera.[2] The number of species in these genera correspond fairly well to Dr. Willis's

[1] The name of *dragonflies* had long been employed in English-speaking countries to designate the entire order of Odonata before its limitation to one of the two suborders (Anisoptera) appeared in publications from Cornell University. It has always seemed to me preferable to continue its older and wider use.

[2] J. B. Smith, *Ann. Rept.*, N. J. State Museum for 1909, pp. 73–82; H. B. Weiss in *Entom. News*, March, 1915, and Jan., 1916; A. S. Nicolay, *op. cit.*, Dec., 1919, and unpublished notes of the present writer.

hollow curves, when their fewness is considered, and are as follows: 25 genera of 1 species each, 6 of 2, 2/3, 5/4, 2/6, 1/9, 1/10, 1/12, 1/17.

A division of the State into six more or less well-defined physiographic regions has been mapped.[3] On listing the species found in each of these regions, only five species (*Lestes rectangularis, Ischnura posita, Anax junius, Libellula pulchella, Sympetrum rubicundulum*) are found in all six. Eleven others,[4] however, are known from five of these regions and it is highly probable that they also occur in all six. All of these sixteen are widespread in North America east of the Rocky Mountains; one of them (*Anax junius*) occurs also in the West Indies, on the Pacific coast of North America, in the Hawaiian Islands and has been reported from Tahiti, Kamchatka and China; another (*Anomalagrion hastatum*) reaches southward to Costa Rica and Venezuela, Cuba, Hayti and the Galapagos Islands; three (*Plathemis lydia, Erythemis simplicicollis* and *Pachydiplax longipennis*) reach British Columbia; the *Erythemis* and the *Pachydiplax* are known from Mexico, the *Erythemis* in the West Indies, the *Pachydiplax* in the Bermudas. On the other hand, certain species which thus far have been found only in one region in New Jersey are almost or equally as widespread (*Lestes congener* and *uncatus, Argia translata, Enallagma ebrium* and *hageni, Ophiogomphus rupinsulensis, Progomphus obscurus,* etc.). In at least some of these cases, we may suspect that the data from New Jersey are incomplete. The important fact for our present purpose is that these sixteen widespread species, even within their respective families, are on morphological grounds of very different ages, *Libellula* for example representing a more primitive condition than *Erythemis, Sympetrum* or *Pachydiplax.*

[3] Smith, *op. cit.*

[4] *Calopt. maculata, Enal. civile, Isch. verticalis, Anomalagr. hastatum, Gomphus exilis, Epiæschna heros, Libellula cyanea, L. semifasciata, Plathemis lydia, Erythemis simplicicollis, Pachydiplax longipennis.*

The only species which from our present knowledge, or ignorance, may be looked upon as endemic in New Jersey are *Enallagma recurvatum* and *Somatochlora provocans*,[5] both of which belong to genera found throughout much of the holarctic region. No genera are endemic.

That group of damselflies which de Selys included in the legion Agrion consists in New Jersey of 33 species belonging to the 8 genera, *Argia* (6 species), *Chromagrion* (1), *Nehalennia* (2), *Amphiagrion* (1), *Enallagma* (17), *Telagrion* (1), *Ischnura* (4) and *Anomalagrion* (1). We have no sufficient geological or paleontological data to determine the relative ages of these genera, but, as far as one may deduce them from morphological considerations, *Argia* would seem to have the best claims to be the most primitive (earlier) and *Anomalagrion* the most specialized (later) genus.

Considering the distribution of these eight genera throughout the world, we find that *Argia* has more than 70 species but is confined to the Americas, *Chromagrion* has but one species extending from Maine and Quebec to New Jersey and Indiana; *Nehalennia* has 7 or 8 species from China, Europe, the United States (3 or 4) and Brazil; *Amphiagrion* has 2 species from the United States and Lake Titicaca; *Enallagma* 50 or more species, chiefly in North America, but some in Europe and northern Asia, and some of doubtful affinity in Africa and southern Asia; the six species of *Telagrion* are, with the exception of the one species from the Atlantic seaboard of the United States, from Trinidad and Brazil; the more than 30 species ascribed to *Ischnura* are from all parts of the world; the distribution of the only species of *Anomalagrion* has already been stated.

Looking only at *the total numbers of species in the world* in these genera, *Argia* would, by one of Dr.

[5] I can not find the data on which Pennsylvania is included in the range of *S. provocans* in Muttkowski's Catalogue of the Odonata of North America, page 132.

Willis's rules, qualify as the oldest, *Ischnura* as much younger and *Enallagma* occupy a position between the other two. The area occupied by *Ischnura,* however, is more extensive than that of either of the other two. In New Jersey, the numbers of species give a different order, viz.: *Enallagma* 17, *Argia* 6, *Ischnura* 4.

It would therefore appear that the areas of distribution of the genera and of the species and the numbers of the species within each genus of the Odonata of New Jersey afford very few hints as to the relative ages of the taxonomic units.

The Odonata are animals with great inherent powers of dispersal and in the United States even the most endemic species occupy relatively extended areas. What has been learned of various species during the last twenty-five years[6] should impose great caution in asserting that any species of Odonata is of very limited distribution.

For these reasons the Odonata make a poor showing when tested by Dr. Willis's hypothesis of *Age and Area* and we turn to another group of Insects in which powerful and sustained flight is not a marked characteristic.

We owe to my colleagues in the Academy of Natural Sciences of Philadelphia, Messrs. J. A. G. Rehn and Morgan Hebard, an interesting and excellent paper on the Dermaptera and Orthoptera of the Coastal Plain and Piedmont Region of the southeastern United States.[7] In it the distribution of the species is tabulated in very convenient form, so that it is possible to take from it with great ease figures which may be compared with Dr. Willis's conclusions. The scope of the paper is Virginia, North and South Carolina, Georgia and northern Florida; 251 species and geographic races be-

[6] For example, up to 1899, *Calopteryx angustipennis* was known only from a single male collected in Georgia by Abbott in the eighteenth century, one female from Kentucky and two other females of unknown provenance. In that year it was found in abundance in western Pennsylvania by Mr. E. B. Williamson.

[7] *Proceedings,* Acad. Nat. Sci., Phila., Vol. 68, pp. 87–314, 3 pls. 1916.

longing to 100 genera comprise the Dermapterous and Orthopterous fauna of these states. They are tabulated both by physiographic regions and life zones and between these two categories a very considerable degree of correspondence exists.

Six species, three of them probably introduced by man, two of them cockroaches, are generally distributed from the Boreal to the Sabalian (or lower division of the Austroriparian) life zone. As the data for the Boreal zone in general are stated by the authors to be very scanty, the following remarks leave it out of consideration.

Seventy-one species are tabulated as confined to one life zone in the southeastern states, but only 32 of these 71 are confined to these states or the immediately adjoining states. The remaining 39 are of wide distribution. The 32 species may be styled "possibly endemic" for convenience here; none of them belong to monotypic genera; 20 of the 32 are of the family Acrididæ (short-horned grasshoppers) and of these 20, 11 belong to the large genus *Melanoplus* (which contains over 200 species but is limited to North America) and the generic areas of the other 9 species are fairly wide although the numbers of species in their respective genera are not nearly so great. We may add that the distribution of the 242 species of the families Acrididæ, Tettigoniidæ and Gryllidæ of the southeastern states into genera forms a hollow curve, incomplete, but approximating those of Dr. Willis. Thus far these Orthoptera agree with Dr. Willis's conclusions quoted but when we attempt to determine the age of genera and species from the present areas of distribution in the southeastern states we seem to be left in the dark. The genera whose species singly or collectively occupy all five of the life zones or four of them (excluding the Boreal on account of the meagerness of the data therefor), and which have the largest numbers of species, should be the oldest, if Dr. Willis's conclusions are sound. There are 11 gen-

era of the Acrididæ which fulfil this condition as to area and their respective numbers of species in the southeastern states range from 1 (*Dissosteira*) to 34 (*Melanoplus*) with an average of 5.6 species per genus. We doubt whether any student of the Orthoptera will regard *Melanoplus* as the oldest genus of Acrididæ in these states. Mr. Rehn tells me that he considers *Podisma* a much older grasshopper. Thirty-one species from North America, Europe and (mostly northern) Asia were catalogued by Kirby in 1910, a greater area, therefore, than that of *Melanoplus*. *Podisma glacialis variegata* is listed by Rehn and Hebard (page 96) as from "High Appalachian summits only." Although paleontological data on Acrididæ are scanty, it is of some interest to note that one *Dissosteira* and one *Hippiscus* are recognized in the European Miocene.[8]

On the principles of *Age and Area* the oldest genera of Tettigoniidæ (long-horned grasshoppers, katydids) in the southeastern states should be *Orchelimum* and *Conocephalus* and the oldest of the Gryllidæ (crickets) *Nemobius*. One species of *Orchelimum* has been listed from the Miocene of Florissant, four of "(*Nemobius*)" from the European Oligocene and two of *Gryllus* (which Mr. Rehn inclines to regard as an old cricket) from the Oligocene and Miocene of Europe.[8] Can the claims of these four genera to high antiquity be accepted from the standpoint of morphology?

The Carabidæ, or Ground Beetles, have still more limited powers of flight than the Orthoptera; 356 species have been listed from New Jersey.[9] The 72 genera, in which they are placed, again form approximately one of Dr. Willis's hollow curves. Species found in five or in all six of the physiographic regions of the State previously mentioned belong to every one of the categories of genera from that with one species to that with 36

[8] Handlirsch, "Die Fossile Insekten," pages 687, 688, 683, 685, 686.

[9] Smith, *l. c.;* Weiss, *l. c.*, and *Ent. News*, April, 1916, May, 1917, and Oct., 1918; Nicolay, *l. c.*

species, but the *proportion* of genera with these *"wide" species within the State* steadily increases from the genera with one species each onward,[10] as one might expect. Between the extent of distribution outside of New Jersey of a "wide" New Jersey species belonging to a genus with a few species (*e.g., Scarites*) and that of a "wide" New Jersey species of a many-specied genus (*e.g., Calosoma, Amara*) there is often little to choose. Some species thus far recorded from only a single locality in New Jersey have a wide distribution outside of the State (*e.g., Lebia marginicollis, Chlænius prasinus, Harpalus convivus*); such cases are probably due to incomplete data. There appear to be no species endemic in New Jersey. The genus with the largest number of species in the State is *Platynus* with 36, followed by *Bembidium* (*Bembidion*) with 23, *Pterostichus* and *Amara* each with 21. The numbers of species in America north of Mexico for these genera are *Platynus* 87, *Bembidion* 369, *Pterostichus* 81 (now under two genera), *Amara* 179 (now under 6 genera).[11] American Tertiary fossils have been referred to 19 species of *Platynus* (1 of them Eocene), 12 species of *Bembidion* (1 of them Eocene), 10 species of *Pterostichus* (Miocene and later) and 6 species of *Amara* (Miocene). European fossils referred to these genera are of no greater age, but one European species of *Carabus* is of the Eocene and a *Galerita* is known from the Eocene of Green River, Wyoming.[12] Dr. Willis would doubtless conclude that *Bembidion* is an excellent illustration of Age and Area. Mr. Leng has kindly written me, how-

[10] The actual figures are 26 genera with 1 species each (6), 16 with 2 (7), 9/3 (5), 2/4 (1), 1/5 (1), 2/6 (1), 3/7 (3), 3/9 (3), 1/13 (1), 1/15 (1), 1/16 (1), 2/17 (2), 1/19 (1), 2/21 (2), 1/23 (1), 1/36 (1). The numbers in parentheses are those of the numbers of genera in each category having one or more species in five or all six physiographic regions of New Jersey. The generic groupings employed in Leng's Catalogue of the Coleoptera of America, North of Mexico, will make some difference in the figures.

[11] Leng's Catalogue cited.

[12] Wickham in Leng's Catalogue; Handlirsch, "Die Fossile Insekten," p. 705.

ever, "the very numerous species of *Bembidion* and allied genera composing the tribe Bembidiini characterized by the stubby, subulate, last palpal joint and other highly derivative characters seem to me very recent. On the other hand, the eight-segmented abdomen and the comparatively soft pubescent elytra of *Brachinus* seem to me like a survival of primitive characters."[13] *Brachinus* has 13 species in New Jersey, 27 in America north of Mexico and to it have been referred two North American and one European fossil species, all of Miocene age. If *Brachinus* be entitled to the veneration which Mr. Leng suggests, its paleontological deficiencies must be shouldered by our long-suffering friend, "The Imperfection of the Geological Record."

It is very true that the areas inhabited by the insects thus far discussed are not sharply defined, as they are more or less arbitrarily designated parts of a great continent. Dr. Willis's results were largely obtained from a study of the floras of islands, especially Ceylon, New Zealand, Great Britain, whose physiographic limits are consequently clear and distinct, but he expressly extends his conclusions to just such continental areas as those which we have considered here for insects, *e.g.*, the flora of Cambridgeshire, the birds of British India, the endemics of Brazil (pp. 236, 237).

To turn briefly to an island fauna, there are 68 species of Odonata recorded from Cuba and the nearby Isle of Pines.[14] They are assigned to 37 genera and exhibit a more perfect hollow curve than any of the three previous cases: 23/1, 6/2, 3/3, 2/4, 2/5, 1/6. Five species are believed to be strictly endemic in these two islands; one of the five is of the monotypic and endemic genus *Microneura* which has morphological claims to being specialized, hence of recent origin; two are of the genus

[13] See also the Introduction to his Catalogue, page 29.

[14] See *Trans. Amer. Ent. Soc.*, XLV, pp. 335–396, 1919; *Biol. Cent.-Amer. Neur.*, Introduction, Table B, 1908; also Kolbe, *Arch. f. Naturgesch.*, Jahrg. 1888, Bd. I, H. 2, pp. 153–178, taf. XIII; Kahl, *Ann. Carnegie Mus.*, X, pp. 519–526, 1916.

Neoneura, which is probably less specialized as a whole than *Microneura* and contains 17 species ranging from Cuba and Texas to southern Brazil; the remaining two are *Enallagma truncatum* and *Progomphus integer,* genera of still wider range, neither of which is apparently very old nor very young. Ten other species [15] are confined to the greater Antilles; two of the ten are of genera not known to extend beyond this group of islands, viz.: *Hypolestes* (with one other species in Jamaica) and the monotypic *Scapanea;* six species are of widespread tropical American genera and the remaining two are of the cosmopolitan *Lestes,* having more than 75 living species. I am disposed to regard *Lestes* as ancient, but this opinion is not universally shared by students of the Odonata, and I should look on *Hypolestes* as still older. *Protoneura* is decidedly specialized by reduction, going beyond *Microneura. Telebasis* and *Erythrodiplax* are not pronouncedly antique or modern; *Perithemis* may be older. *Dythemis, Scapanea* and *Macrothemis* seem of recent origin—all this, of course, on purely morphological evidence.

Incidentally, an unexplained riddle in geographical distribution is why the large and apparently strong *Scapanea frontalis,* with the favoring trade wind, has not been found on the mainland to the west. Considering it and the feeble flight of *Anomalagrion hastatum,* whose wide range has been given earlier in this paper, we are impressed with the fact that power of flight alone does not determine the dispersal of dragonflies. *Scapanea* and *Anomalagrion* are both monotypic, both have near allies, both appear to be specialized, and hence relatively recent forms, within their own families, yet their respective areas differ greatly in extent, that of the tiny *Anomalagrion* including all of the territory in which *Scapanea* is found and very much more beyond.

[15] *Lestes spumaria, L. scalaris, Hypolestes trinitatis, Protoneura capillaris, Telebasis vulnerata, Dythemis rufinervis, Scapanea frontalis, Macrothemis celeno, Erythrodiplax connata justiniana, Perithemis domitia domitia.*

Here in the Odonate fauna of Cuba, as in the examples previously given, I fail to find the key to the origin and evolution of species with the ease which Dr. Willis's commendation of Age and Area would lead me to expect and which I would welcome if the key but turned in the lock.

THE DISTRIBUTION AND DERIVATION OF SOME NEW ENGLAND ECHINODERMS

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ALTHOUGH naturalists no longer question the belief that existing species are the descendants of earlier forms by some process of evolution, there is still a considerable body of popular dissent encouraged by ignorant, even though often well-meaning, leaders. It is therefore worth while to marshal all the facts that can be of service in demonstrating the truth, and this is my excuse for offering the following statement concerning the distribution of New England echinoderms. The facts are not offered as new nor are the conclusions surprising, but both may be of use in confirming our faith in organic evolution.

Of the 46 species of echinoderms known to occur on the New England coast, there are at least half a dozen (all holothurians) concerning which our knowledge is too incomplete to permit us to discuss their distribution, but of the remaining 40, we know enough to warrant the attempt to interpret their derivation in the light of their distribution. Of these 40, 32 are certainly allied to a northern fauna, while 8 seem to represent a southern group. Naturally enough, the northern forms reach the southern limit of their distribution on the New England coast; few of them occur south of Nantucket and then only in deep, cold water. And of course, the southern forms find their northern limit along the southern

coasts of Massachusetts, only one or two occurring north of Cape Cod.

Perhaps the best example of the northern group is the common green sea-urchin of the Maine coast (*Strongylocentrotus dröbachiensis*) whose scientific name has so long served as a stumbling-block to the zoological beginner and an awful example of much that a technical name should not be! The distribution of this urchin is very extensive; it is practically circumpolar in the Arctic regions though there are areas, both on the American and Siberian coasts, where it has not yet been taken; on the eastern side of the Atlantic, it comes as far south as Denmark and Scotland regularly, being common on those coasts, and it has been recorded from Holland, from the English Channel and even from near Madeira, in 100 fms.; in the western Atlantic, it ranges southward at least to Nantucket and in deep water to New Jersey and has been reported from as far south as Florida; in the eastern Pacific, it occurs regularly as far south as Oregon and specimens in the Museum of Comparative Zoology are labelled, on excellent authority, as from Hilo, Hawaii;[1] finally, in the western Pacific, it ranges to lat. 38° N. on the eastern coast of Japan and to lat. 37° N. in the Sea of Japan. Its bathymetrical range is from tide-pools to a depth of 1600 m. while its temperature range is even more remarkable, as it has been taken in water where the temperature was only 29.8° F., and yet it occurs abundantly in water of 50°–56°. It is not strange that having so wide a range, in every sense, the green sea-urchin is very variable and shows remarkable diversity in form and color and even in certain structural details, which may be associated with peculiar-

[1] The specimens reported from near Madeira and from Hilo are difficult to account for, but in view of the remarkable temperature-range of *dröbachiensis* it is not absurd to suppose that they may have been carried to those warm spots on the foul bottoms of vessels which had been for some time previously in Scottish or in Alaskan ports. It seems probable that the specimens found at Hilo were dead when picked up along shore, the warm harbor water proving fatal after their long journey from colder seas.

ities of habitat. And yet neither on the European or American coasts is there any constancy in these peculiarities and no varieties are recognized nor is any closely related species of the genus known. In the Pacific, on the other hand, we find a very different state of affairs. The genus is almost certainly of North Pacific origin and there seems no reason to doubt that *dröbachiensis* has spread both eastward and westward from the northern end of Behring Strait. On the coasts of Japan are at least four other members of the genus and two or possibly three more occur on the Pacific coast of North America. But the specific limits of some of these species are ill-defined and their separation from *dröbachiensis* is not always clear cut. In the north, among the Aleutian and Kurile Islands, all the Strongylocentroti are either *dröbachiensis* or so very closely allied that their distinctness is open to grave doubt. But the farther south one goes in either the western or eastern Pacific, the more evident is the segregation of distinct forms. Off the coast of Oregon and California, in moderately deep (85–850 m.) and moderately warm (56.5°–41°) water, there is a well-marked species, *S. fragilis* Jackson, the distinctive features of which might be produced by carrying to an extreme some of the characters shown by deep-water specimens of *dröbachiensis*. Thus the spines are relatively long, slender and brittle, the test is thin and fragile and the color is more or less red orange, though the test is often purple. No one who compares specimens of *fragilis* with a good series of *dröbachiensis* from the coast north of Oregon can have any doubt of a genetic connection. There may be room for difference of opinion as to whether the remarkable variability of *dröbachiensis* is the cause or the effect of its extraordinary geographical, bathymetrical and thermal range, but there is no doubt of their correlation and there is therefore unusual material and opportunity for the formation of new species.

Many other boreal echinoderms show a distribution

and a variability more or less similar to that of the green sea-urchin. Lack of space forbids taking these cases up in detail but a few of them may be mentioned. The so-called sun-star, one of the characteristic sea-stars of the Maine coast, *Crossaster papposus,* has almost precisely the same range as *Strongylocentrotus dröbachiensis,* though it occurs normally farther south and west on the British coasts. Crossaster too like Strongylocentrotus is a north Pacific genus with only the single species in the north Atlantic. Our American authority on sea-stars, Dr. Walter K. Fisher (1911, Bull. 76, U. S. Nat. Mus., p. 326), says of *C. papposus:* "The North Pacific specimens are also variable, so much so in fact, that the extremes are very unlike. The species tends to form small varieties differing with locality and also with depth. . . . The forms listed herewith as . . . *papposus* may in reality be small species but it has not been possible to separate them on account of intergrades. With the exception of the Japanese specimens, which are believed to constitute a distinct species, all the North Pacific varieties have been called . . . *papposus.*" This is strikingly similar to conditions in Strongylocentrotus.

Among the brittle-stars, there is a case of distribution and differentiation into varieties, subspecies and species, of the same sort as the two first given. The so-called daisy brittle-star (*Ophiopholis aculeata*) is one of the most abundant echinoderms of the New England coast. Its distribution differs from that of the green sea-urchin and the sun-star only in a further extension southward on all coasts. The gaps on the North American and Siberian coasts, where specimens have not yet been taken, are conspicuous but may well be due to our imperfect knowledge of those regions. Although so very variable on the Arctic and Atlantic coasts of Europe and America that hardly two specimens are exactly alike, it is impossible to distinguish any constant varieties. In the north Pacific, however, we find not

only recognizable subspecies of *aculeata,* but other species of the genus. On the American side there is a warm-water species (*bakeri*) and a cold-water species (*longispina*) which are closely related and on the Japanese side, too, there is a similar condition, with the warm-water *mirabilis* and the cold-water *brachyactis.* Differentiation into constantly distinct forms has gone further in the daisy brittle-stars (*Ophiopholis*) than in the sun-stars (Crossaster) but not quite so far perhaps as in Strongylocentrotus.

Among holothurians both *Chiridota lævis* and *Cucumaria frondosa* show peculiarities of distribution that warrant our believing their derivation and extending range correspond to those of the urchin, sea-star and brittle-star already cited. It must be said however that specific limits in these two holothurian genera are still very hazy and it is unwise in the present state of knowledge to lay any stress on evidence which they might seem to afford.

Turning now to the group of southern species, the most interesting case is the brown sea-urchin of Woods Hole (*Arbacia punctulata*). The genus Arbacia seems to have originated on the west coast of tropical America, where two species (and a third in a closely allied genus) still exist. Passing eastward during the time when there was open connection between the Pacific and the Caribbean, Arbacias finally reached the coast of Brazil, the west coast of Africa, the Mediterranean and even, far to the southeast, the isolated islet, Tristan de Cunha. But the species now occupying the Brazilian, Mediterranean and African coasts are not the same as the one which first entered the Caribbean Sea. If that one still persists, it is as *punctulata,* the Woods Hole species; if extinct now, as is quite likely, the Woods Hole Arbacia is its nearest living ally. The remarkable thing about the distribution of *punctulata* is not that it has gradually extended its range northward to the southern coasts

of Massachusetts and eastward to Trinidad and Tobago, but that it seems to be entirely wanting from Jamaica and from the Lesser Antilles. It is said to occur on the northwestern coast of Cuba and there is a dubious record from Hayti, but if these records are correct, these localities no doubt received their Arbacias from the Tortugas and Florida or possibly from Yucatan. As *punctulata* has a very limited bathymetrical range, there is no reason to doubt that it has spread along shores and has not crossed wide areas of deep water. Hence the Tobago and Woods Hole Arbacias have been geographically diverging ever since their ancestors set out eastward and northeastward from the Panamic region. Yet specimens from these two extremes of the present geographical range show no characters by which one can be separated from the other even as a variety. It is interesting to note that specific limits in the genus Arbacia are very constant, and (with perhaps one exception) none of the species show very much tendency to vary. This fact is especially noteworthy in connection with the environmental changes which Arbacia endures in Vineyard Sound and Buzzards Bay. There, in severe winters, there is no question that large numbers are destroyed by cold and living specimens are rare the following summer. The survivors in a few years however replenish the region and Arbacia again becomes common. There is no evidence that this process, no doubt repeated often in a century, has as yet led to any visible, structural modifications. Arbacia, which is a relatively old type of sea-urchin, contrasts strikingly in this respect with Strongylocentrotus, a relatively recent and specialized urchin, changes in which seem to occur very easily in association with environmental changes.

One other of the southern species warrants a word because it is perhaps our commonest New England echinoderm, and its history is probably the reverse of Arbacia although, like the brown sea-urchin, it ranges

from Woods Hole to Florida. This is the common sea-star of Massachusetts (*Asterias forbesi*), not the common sea-star of the Maine coast, which is *A. vulgaris* and very probably identical with *A. rubens* of Europe. Of course, it is well known that the ranges of *forbesi* and *vulgaris* overlap and it is a common belief that the two species hybridize. But if such hybrids occur they must be very rare, for there are no authentic specimens on record or extant, so far as I know. Neither do I know of any satisfactory record of the production of hybrids of the two species artificially, though it would seem to be an easy thing to do. A comparison of the distribution and habitats of *vulgaris* and *forbesi* shows clearly that *vulgaris* is a lover of cold water, while *forbesi* prefers higher temperature. So when *vulgaris* is found south of Cape Cod, it is normally only in deep, cool water (local conditions of course determine the depth) while the localities north of Cape Cod where *forbesi* occurs are shallow bays or inlets where the temperature is moderately high. So closely related are *forbesi* and *vulgaris* that young specimens can be told apart only with difficulty and by careful examination of seemingly insignificant details. It seems highly probable that *forbesi* is the direct descendant of *vulgaris;* that it is a species developed in connection with the warmer waters of the coast from Massachusetts southward. It is not necessary to assume that temperature has been a determining factor, for it may be that the range southward is due to inherent traits that permit occupation of a warmer area. In other words, the southern range may be the *result* of certain characters, rather than the *cause.* But whether cause or effect or neither, the occupation of the warmer area is associated with the fixing of certain relatively insignificant external characters, so that we recognize *forbesi* as a distinct species. No species of Asterias, *sensu strictu,* occurs south of the range of *forbesi* and its origin from the north seems therefore almost certain.

One other New England echinoderm deserves consideration as it illustrates discontinuous distribution, and represents a stage of evolution beyond that shown by Strongylocentrotus and Crossaster. This interesting case is the common synaptid of Cape Cod and Woods Hole (*Leptosynapta inhærens*), which is found not only on the New England coast, but on the northern and western coasts of Europe, on the western coast of the United States and in Japan. Comparison of specimens from Norway, Ireland, Italy, Massachusetts and California shows such close similarity among them that it seems impossible to doubt that they are all one species. Nevertheless, no Leptosynapta is known from the Arctic coasts of Asia or America and there is no reason to believe that any now occur there. What does seem probable is that, when in earlier geologic times the climate of the polar regions was mild, *inhærens* was a circumpolar species. As the climate became colder and more severe, the synaptids retreated southward along the coasts of all the continents, and those occupying the cooler areas still retain their common specific characters and we call them all *inhærens*. But on all coasts as the synaptids came into warmer waters, diversification has occurred. In European waters, four species at least have become differentiated from the original stock. On the eastern coast of America and in Bermuda and the West Indies, at least seven species have separated from each other. On the southern coasts of Japan is a well-marked species which has extended its range to East Africa on the southwest and to the Gilbert and Loyalty Islands on the southeast, while in Torres Strait another species occurs and two others occupy the southern shores of Australia.

Several other species of New England echinoderms offer interesting data regarding distribution but as each of these is similar to one or the other of the cases already cited, they need not be detailed here. The dis-

tribution of our echinoderms seems to indicate beyond doubt that, with a few noteworthy exceptions, they are of northern origin, that they have little tendency to form endemic species or varieties on our coasts, but that they are representatives of genera that in warmer seas or under more favorable conditions become differentiated into more or less numerous, constant, recognizable forms.

SOME FACTS RELEVANT TO A DISCUSSION OF THE ORIGIN AND INHERITANCE OF SPECIFIC CHARACTERS

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IT seems reasonable to suppose that the geographic races or "subspecies" of mammals and birds represent early stages in the differentiation of species. The differences by which these local races are distinguished from one another appear to be of the same type as those which distinguish "true" species, and indeed the differences are, in many cases, of equally great magnitude. The assignment of a given race to the rank of a subspecies, rather than to that of a species, is due to the circumstance that it intergrades with other similar races, in all its characters, and this fact, in turn, depends entirely upon historical accident. The intergrading forms, in the one case, chance to have been preserved, in the other to have been eliminated.

When we compare the various subspecies constituting some widely ranging species, we find that they commonly differ in a considerable number of characters. In the case of mammals and birds at least, the subspecies do not differ by single characters of the presence-and-absence type, such as distinguish various "mutant" strains from one another or from the wild species. Indeed, the number of these recognizable differences commonly increases as we subject our material to more and more intensive inspection.

Furthermore, the differences under consideration are mainly of a statistical nature. While the most divergent of these subdivisions of a species may be so distinct from one another that their frequency "polygons" for certain characters show little or no overlapping, this is not true of the more closely related ones. Here, the frequency

distributions for every character may overlap broadly, so that the differences must, in every case, be expressed in terms of averages. For this reason a taxonomist may hesitate to assign a given specimen to one or another "subspecies" until he is informed as to the locality from which it is taken. Such an attitude may appear unwarrantable to one who fails to recognize that subspecies are statistical and not logical concepts.

Again, the subdivision of a wide-ranging species into a definite number of geographic "subspecies" can be justified only on the further assumption that we are dealing with populations of relative homogeneity, which replace one another more or less abruptly along definite lines of demarcation. Were we concerned with one continuous population, showing insensible gradations throughout its entire range, there would be no warrant for recognizing any special number of subspecies nor for distinguishing any particular set of boundaries between their respective territories. To what extent, in general, the recognized subdivisions are arbitrary and to what extent they are natural, I am not in a position to state, nor even to form a well-grounded opinion. I may say, however, that certain test cases within my limited experience serve to give me confidence in the general validity of some of these subdivisions.

Before entering into any discussion of the nature of the differences between our subspecies, it is necessary to satisfy the natural skepticism of those who may be disposed to doubt whether we are dealing with characters which are "genetic" or hereditary at all. Many organisms are differently influenced by different environments, within the limits of the individual lifetime. May this not be true of the subspecies of mammals and birds, which inhabit regions frequently differing widely in respect to their climatic conditions? For one genus of rodents (*Peromyscus*) I have offered detailed disproof of such

a contention in several previous papers,[1] and the evidence is, if possible, even more conclusive now. Several geographic races, from extremely unlike environments, have been reared together at La Jolla for from two to ten or more generations. Thus far no appreciable convergence of these types has occurred.

After one has completed the preliminary task of describing as many of these local populations as possible, with the greatest thoroughness attainable, he may feel that he has qualified himself, in a slight measure, to attack some of the various problems which arise in connection with them. Are any correlations to be discovered between these subspecific differences and factors of the environment? And aside from such correlations, is any law whatever discoverable in the arrangement of these subspecies with reference to one another? Again, do these complexes of characters which distinguish the different geographic races tend to vary together as we pass through the entire range of the species, or do the component elements change quite independently of one another? Finally, how do these subspecific characters "behave" in heredity, either in relatively pure strains of the single races, or in hybrids between different races?

The first two of these questions are ones which may be answered, in a certain measure, without recourse to breeding experiments, nor to a special mathematical technique. My own small claim to speak upon this phase of our subject is based in part upon my studies of mice of the genus *Peromyscus,* but even more upon information which I have been able to acquire through the labors of certain other students of mammals and birds.

A very little inspection suffices to show that these local races are not arranged at random. Certain general trends of geographic variation are so obvious that they have long been recognized. Among these the fore-

[1] AMERICAN NATURALIST, November, 1915; *ibid.*, March, 1917; *ibid.*, April–May, June–July, August–September, 1918; *Journal of Experimental Zoology,* April, 1920.

most is doubtless the trend which seems to establish a definite positive correlation between atmospheric humidity and pigmentation. In the "Pacific Slope" area of North America, this law is evident when we pass from the relatively arid interior to the moist fog-laden atmosphere of the sea-coast. It is also evident as we pass from the coast of southern and lower California to that of Oregon, Washington and Alaska.

This increase of pigmentation shows itself in the general darkening of the color-tone of the plumage and pelage, as well as in the expansion of the pigmented areas, and the correlative decrease in the size of the white areas. In *Peromyscus,* the darker races—at least in certain cases—are likewise found to have more pigment in various regions of the naked skin. This is true of the soles of the feet, the ears, the snout and the scrotum. On the basis of evidence which is not yet entirely adequate, I conclude provisionally that these different pigmental characters have varied together, geographically speaking. On first thought, such a situation might be regarded as an almost inevitable one, due to a seeming tendency for pigmentation, in all parts of the same individual, to vary in the same direction. That no such general tendency has been responsible for the facts will be shown to be probable later.

When we seek for a mechanism to account for this agreement between the climatic gradient and that for pigment formation, we are forced to admit that decisive evidence is not yet forthcoming. The most ready explanation at hand is the naïve one that, in some way, atmospheric humidity favors the chemical processes responsible for pigment formation. This explanation would not necessarily involve any Lamarckian assumptions as to inheritance, and furthermore it is supported by certain experimental evidence which is, it is true, very fragmentary. Reference may be made, in particular, to the experiments of Beebe,[2] in which the plumage of birds

[2] *Zoologica:* New York Zoological Society, 1907.

of several species was caused to become darker, apparently owing to the effects of increased atmospheric humidity; likewise to certain results of Morgan,[3] who observed several specimens of *Peromyscus* which had become very pale, as the possible result of greatly decreased humidity.

Such an explanation is not, however, borne out by the results of transplanting several exotic subspecies of mice to La Jolla, where, as already stated, they still maintain their characteristic color differences, even after a considerable number of generations under identical conditions of environment. Nor is it supported by the outcome of various "natural experiments" of perhaps much greater duration, which have been reported by certain naturalists. Grinnell and Swarth,[4] for example, have noted the occurrence of a subspecies of song-sparrow (*Melospiza melodia cooperi*), proper to the coastal region of southern California, which has extended its range into a canyon on the eastern (desert) slope of the San Jacinto Mountains. Yet here, in a region of great summer heat and extreme aridity, it has retained the dark plumage of the subspecies *cooperi,* and has not varied in the direction of the desert race *saltonis.*

I can not, however, regard such negative evidence as decisive in the present instance, owing to the possibility that the invading race may be continually recruited from its normal habitat on the western side of the mountains. Moreover, certain similar evidence, based upon the influx of the English sparrow into Death Valley, is at present somewhat equivocal.[5]

The chief alternative explanation of these pigmentation gradients in nature would invoke the principle of selection. We might, on the one hand, take refuge in the theory of concealing coloration, and this theory has a certain *prima facie* plausibility, particularly as applied

[3] *Annals N. Y. Academy of Sciences,* 1911.

[4] University of California Publications in Zoology, Vol. 10, 1913.

[5] Grinnell (unpublished Ms.)

to the pale hue of so many desert animals. I have, however, recently argued against this type of explanation, which is beset by some serious difficulties.[6] Another application of the selection principle would rest on the supposition that these varying degrees of pigmentation were, in themselves, of no service to the organism, but that they were indices of different constitutional tendencies. The type of organism best adapted to desert life might be supposed to produce little pigment, and that best adapted to coastal fogs might be supposed to produce much pigment.

It is obvious that a problem of this nature can only be solved experimentally. I may state that I have already commenced experiments in which the animals are being subjected to an artificial environment involving a much more extreme change of life conditions than is involved in the transplantation of exotic races to the unmodified atmosphere of La Jolla.

Some of the most conspicuous of our subspecific differences relate, however, to characters other than pigmentation. In this connection we must include not only differences in the absolute size of the body, but more particularly ones in the proportional size of various parts—the tail, feet, ears, and certain bones of the skeleton.

Here, too, we find that the various grades in the development of these parts are not arranged purely at random. There are, throughout wide expanses of territory, fairly consistent trends, in the direction of an increase or a decrease in the size of body as a whole, or in the relative size of one or another member. But, unlike the case of pigmental characters, no general law seems to be discernible here. When the data are viewed broadly, no certain correlations seem possible between differences in the proportional size of parts and definite factors of the physical environment. Indeed, contradictory tendencies may be shown by different, closely re-

[6] *Journal of Mammalogy*, May, 1921.

lated organisms, or even within different parts of the range of a single subspecies.

Although it is not the object of the present paper to discuss in detail the evidence on which the foregoing statements are made, a single illustration may be worth while. In the species *Peromyscus maniculatus,* with which my own studies have been chiefly concerned, there is a marked increase in the length (relative and absolute) of the tail and foot, as we pass northward, along the Pacific coast, from San Francisco Bay to Alaska. But from San Francisco Bay southward to the Mexican border, as well as eastward into the arid interior, the length of these members undergoes no decrease. Indeed, the mice of the Coronado Islands, near San Diego, have feet (though not tails) far longer than those of the neighboring mainland—as long, in fact, as those of mice from Humboldt Bay, at the opposite end of the state. Other erratic features in the geographic variation of these animals could be cited, even within the limits of the state of California.[7]

Facts of this class are obviously not in accord with certain generalizations which have been proposed as to the behavior of bodily proportions, in relation to climatic or geographic gradients. J. A. Allen's principle of the "enlargement of peripheral parts under high temperature or toward the tropics"[8] is certainly not applicable to the genus *Peromyscus* on the Pacific coast. Far from becoming enlarged, there is, as we have seen, a fairly steady decrease in the length of certain "peripheral parts," as we pass from Alaska to San Francisco Bay. Nor do the ears of these mice become longer, in passing either to the south or to the interior deserts,

[7] For birds, Swarth has recently discussed a number of groups which illustrate the independent variation of different characters geographically, as well as their inconsistent behavior in relation to climatic factors. (See especially *Proceedings of the California Academy of Sciences,* Vol. 6, 1916, University of California Publications in Zoology, Vol. 21, 1920.)

[8] Annual Report Smithsonian Institution for 1905 (1906). (Reprinted from the *Radical Review,* 1877.)

as is said to be true of various other mammals. Mice from the vicinity of Humboldt Bay in northern California were found to have ears as long as, or longer than, those from the Mojave Desert.

Indeed, these last named features in the geographic variation of *Peromyscus* are quite out of harmony with the supposition that they have been due to the direct action of the physical environment. My earlier experiments with white mice[9] showed that the length of the tail, feet and (doubtfully) the ears was considerably increased under the influence of high temperature and low relative humidity. If these differences among geographic races in nature depend in any way upon local differences in environmental factors, the relationships must be indirect and obscure. In the present state of our knowledge, any assertion that such relationships exist, and particularly any contention that the subspecific characters of animals are necessarily adaptive, must be dogmatic in the extreme. Indeed there are strong reasons for doubting the reality of any such nicety of adjustment as is implied in speculations of this sort.

The existence of graded series in space,[10] in cases where neither adaptive modification through selection nor the direct influence of environment seems probable, might be accounted for in two principal ways. (1) It might be supposed that, for some reason, distinct races had originated at the two points farthest removed from one another, just as they have arisen on separate islands or other regions more or less separated by barriers. Subsequently, these two races may be supposed to have diffused into the intervening territory and mixed in varying proportions through hybridization. Such a process

[9] *Journal of Experimental Zoology*, Vol. 7, 1909, Vol. 18, 1915.

[10] Such series are by no means confined to mammals and birds. Gulick (Carnegie Institution Publication No. 25, 1905), in his study of Hawaiian land snails, found widely divergent species occupying points far removed from one another, these being connected, however, by numerous intermediate types. This was true in cases where corresponding environmental gradations were entirely lacking.

might ultimately result in a gradation of characters throughout the entire territory involved. It would not even be necessary to assume that the intermediate tract was ever entirely devoid of a population. The two most widely separated points, owing to their offering more favorable conditions of life, might become "centers of distribution," from each of which the preponderant migration would be centrifugal.[11]

The only unexplained circumstance here would be the primary differentiations at the two extremes of the series, but this would not necessarily involve the assumption that the characters produced were specifically adapted to the respective habitats of these two races. On the contrary, it has been contended by a number of writers that any two small samples of a single species would, if isolated from one another, tend to develop along divergent lines, regardless of any differences in their respective habitats.

(2) We might have recourse to the principle of "orthogenesis," which, under various forms, has been espoused by a considerable number of biologists, particularly, in recent years, by paleontologists. It has been contended that a species has the same inherent tendency to vary in certain directions that a developing egg has to develop in a definite specific way. The realization of this particular trend is conceived of as being largely independent of peculiarities of the environment. Such a view would, of course, be invalidated were it shown that this apparently orthogenetic trend were the result of selection by the conditions of life. In some instances, however, such a selective process seems to be pretty definitely ruled out. Among others, may be cited those cases, already discussed, in which the same variational gradient is associated with quite different, perhaps even reversed, environmental gradients. Cases of this sort undoubtedly suggest the existence of definitely directed trends of variation. There need, however, be no ele-

[11] Grinnell (*Auk*, July, 1904).

ment of mysticism in such a view. It is only when these directed trends of variation are assumed to make for higher development or increased adaptation that we may begin to suspect the scientific validity of such a hypothesis.

Now, some of these seemingly "orthogenetic" series appear to be arranged in space, rather than in time.[12] Cases may be cited in fact, in which the degree of modification in a given direction seems to be a linear function of the geographic distance between the races in question. It is not impossible, however, that this spatial arrangement may be fundamentally a chronological one. Thus if the manifestation of predetermined trends of variation should coincide with the dispersal of a species from some common center, we should have just such geographically graded series as we actually encounter. And this explanation would be in no way contradicted by the existence of considerable areas throughout which the characters in question were relatively stable, *i.e.*, the "ranges" of the various "subspecies."

Either of the foregoing views as to the origin of graded geographic series in nature must be regarded as highly speculative at the present time. And it must be recognized that the only thing which would be accounted for in either case would be the existence of *graded series*. Regarding the origin of the character differences themselves, we should still be completely in the dark.

The relation of such views to the modern theory of mutation should here be referred to. So far as I can learn, this theory affords no mechanism, aside from selection, competent to account for these correspondences between structural and geographic gradients. Not only are most recent mutationists very skeptical as to the

[12] Swarth ("Revision of the Avian genus *Passerella*," University of California Publications in Zoology, Vol. 21, 1920), writing of certain races of fox-sparrows, suggests the possibility of "a predetermined line of evolution—as regards direction through space, however, rather than through time."

specific effect of any given type of environment upon the nature of the resulting mutations, but there are reasons for doubting the efficacy of even extreme environmental changes in increasing the number of mutations *of any sort*.[13] Furthermore, it has been contended by Morgan and other writers that the various gradations in the modification of a single genetic factor do not tend to arise in any particular order. An extreme mutant condition, *f*, is as likely to arise directly from *a* as it is from *e* or from any intermediate member of the series.

It may be held, however, that the varying grades of difference between these local races, in respect to any single character, depend upon the action of a varying number of cumulative ("multiple") factors, having identical or closely similar effects. If this be true, as is indeed possible, we should still have to account for the correspondence between the number of these factor differences and the distance apart of the respective races in space. This correspondence might perhaps be explained on the basis of the varying periods of time which had elapsed since the separation of the given races. Such an explanation would, however, be practically identical with the "orthogenetic" one already referred to, and would certainly be unacceptable to many mutationists.

If, therefore, we are dealing in nature, with the same class of factor changes which have been studied so intensively by the Mendelians, any correlations between these changes and environmental conditions or geographic distribution must be the result either of natural selection or of some unexplained tendency toward definitely directed variation ("orthogenesis"). But reasons may be given why selection, in some of these cases at least, is a highly improbable explanation of the facts, while the acceptance of orthogenesis would involve a

[13] Recent unpublished studies on *Drosophila*, conducted at the University of California, by Dr. Margaret Mann, greatly strengthen such doubts.

radical departure from the mutation theory as originally conceived.

Before proceeding further, we must give some attention to the important problem of the correlation of these various characters with one another. By correlation I here denote the tendency of two characters to vary together, either (1) in the same race, or (2) in the same individual.

Let us consider first the question: To what extent do these different characters, which are subject to local variation, tend to vary in the same or opposite directions as we pass from one race to another? Is there, in other words, any tendency for entire complexes of characters to be shifted together? As already stated, we find that the three pigmental characters of *Peromyscus* which have been subjected to quantitative determination do seem to be correlated with one another geographically. These are the general coat color, the width of the dorsal tail stripe and the depth of pigmentation of the soles of the feet. Aside from these, it seems impossible to discover any general law in the geographic behavior of the subspecific characters of these animals. Certain differential characters of the component subspecies may, it is true, undergo simultaneous change throughout a part of the range of a species, but the association between these same characters is found to be entirely dissolved when we pass to other parts of its range. It has been pointed out that the length of tail and foot in one species of *Peromyscus* increases in a parallel fashion from San Francisco Bay northward to Alaska, while elsewhere such a correlation seems to be lacking.

Secondly, we may consider *intra-individual* correlation. To what degree do these measurable characters of our animals tend to vary together *among the members of a single local race?* This is naturally of particular interest in respect to those characters which are subject to geographic variation. It must be emphasized that we are considering here correlations which are independent

of the general size of the body. In a series of animals of varying size, it is needless to say, correlations will be found to exist between almost any two parts.

In an earlier paper I pointed out the existence of a well-marked intra-individual correlation between tail and foot length, and I have recently computed coefficients for certain additional pairs of characters which are involved in the subspecific differences between these mice. In these studies, both the "pure" races and hybrid material has been employed. A moderate degree of positive correlation (about 0.3) is found to exist between the shade of the pelage and the width of the tail stripe, but there is no satisfactory evidence of a correlation among any of the other characters considered. Indeed for certain pairs of characters, the evidence seems sufficient to justify the positive conclusion that no appreciable correlation exists.

Now it is possible that certain of these facts of intra-individual correlation have some bearing upon those of geographic variation. It has been pointed out that the three pigmental characters which I have measured in *Peromyscus* seem to form parallel gradients in nature, and that these gradients correspond fairly well with the climatic gradient, particularly as this relates to atmospheric humidity. The fact that two of these pigmental characters (width of tail stripe and darkness of pelage) are found to be correlated in the individual might be held to account for their coincident modification among the various subspecies. To resort to the familiar conceptions of modern genetics, these two characters might be supposed either to have, in part at least, a common factorial basis, or they might be supposed to depend upon factors which were more or less closely linked. In either case, these various coincident modifications could be regarded as manifestations of a single process of variation.

As regards the third of these pigmental characters—foot pigmentation—the evidence thus far speaks for a

complete absence of correlation between this and the other two characters just referred to.[14] If this lack of correlation is rendered certain by the study of further material, and if a general correspondence with the climatic gradient is fully substantiated, we shall be forced to the conclusion that *these two characters have been independently modified along parallel lines.* Since the tendency to parallel development can not, in this case, be found within the organism itself, its source must be sought in the environment. There must be environmental agencies competent to influence (by selection or otherwise) the degree of pigment formation, regardless of the part of the body affected. On the other hand, it is plain that the existence of a correlation between two characters in the individual is not, in itself, sufficient to insure a constant correlation, geographically speaking. It has just been pointed out, for example, that an increase in the foot-length of a race may or may not be associated with an increase of tail length.

The modern student of genetics is disposed to look upon hybridization as the single fruitful method by which to attack his problems. While I can not subscribe to such an extreme view as this, I have recognized the necessity of crossing various subspecies of *Peromyscus.* Although even very widely different races yield offspring as fertile as those derived from pure races, these experiments have been beset by various technical difficulties which I can not discuss here.[15]

My chief results are based upon two series of hybrids between the most widely unlike races found in California (*rubidus* and *sonoriensis*) and one series between the more closely related *rubidus* and *gambeli.* F_1 and F_2

[14] A positive correlation of + 0.071 was obtained. This is based upon 18 different groups of specimens aggregating 779 individuals. The separate group coefficients range from — 0.32 to + 0.47, there being 10 positive figures and 8 negative ones.

[15] These relate, in large part, to the generally detrimental effect of captivity upon wild species of mice, manifesting itself in a frequent impairment of fertility, stunting of the body, and sometimes in actual deformity.

generations were obtained, but very few back-crosses or later generations of hybrids. The resulting series have been measured and analyzed statistically in reference to the behavior of a considerable number of characters.[16]

Let me point out, before proceeding further, that none of the parent races with which I have dealt has been even approximately "pure," in the sense in which this term is customarily employed by geneticists. Each is a mixture of genetically distinct strains. As evidence of this may be cited the wide range of variability within each race, and the fact that for several different characters these variations are found to be in part hereditary. This has proved to be true of relative tail length, width of tail stripe, depth of foot pigmentation and grade of coat color, as revealed by the computation of coefficients, both for parent-offspring and fraternal correlation. The former coefficients average $+0.27$, for these four characters, the latter $+0.43$.[17]

This "mixed" character of the parent races employed in these crosses should not, however, affect the general significance of the results. For there would, in general, be far more factorial differences between representatives of two geographic races than between individuals of the same race. The F_1 generation from such a cross would present far more heterozygosis than either parent race, taken by itself, and the chances of the segregation of extreme types would therefore be much better in the F_2 than in the F_1 series.

Despite numerous exceptions and inconsistencies, the general statement may be made that both hybrid generations gave intermediate values for the various subspe-

[16] A paper giving a fairly full account of the results of these experiments is now in press.

[17] It is of interest that the correlation between the F_1 parents and their F_2 offspring averages considerably *higher* than that between the parents of "pure" race and their F_1 offspring. Other things equal, the former coefficients should be *lower*, if we had to do with a Mendelian segregation of these characters in the F_2 generation. I am not, however, disposed to attach any great significance to the difference here referred to.

cific characters, while the variability on the whole was greater in the F_2 than the F_1 generation. Not only does the entire complex of characters which serves to distinguish one subspecies from another fail to behave as a simple Mendelian unit character, but the various components of these complexes—the separate characters, taken singly—fail so to behave.

Now this is a picture which has often been encountered by those who have dealt with so-called "quantitative" characters in hybridization, and is the one which the well-known "multiple factor" theory was invented to explain. Indeed, it is quite certain that most geneticists will hail these results of mine as an excellent illustration of the applicability of this principle to the natural varieties of a wild species of mammal.

This may, indeed, be a correct interpretation of my results. But before reaching any settled convictions on this subject, I should strongly advise that we consider all of the evidence. Some of the awkward facts of the case are: (1) This increase in F_2 variability relates not only to characters in respect to which the parent races differ, but is equally evident among characters in respect to which the parent races do not differ. (2) It fails to appear in certain cases where the parent races differ widely. (3) The increase is perhaps shown most consistently in relation to a series of characters (indices of bilateral asymmetry), which, we are able to show, are not hereditary at all.[18] These results can not be adequately interpreted without considering various circumstances which it is impossible to discuss in the present paper. But they seem to furnish very doubtful support for the theory of multiple factors, as applied to the subspecific characters of these mice.

It is, of course, well known that experimental breeders before the days of Mendel fully recognized the high variability of hybrids subsequent to the first generation. But it may be contended with much truth that to substi-

[18] Sumner and Huestis, *Genetics*, September, 1921.

tute vague, unanalyzed tendencies of this sort for a consistent scientific explanation would be a distinct step backward. Still, it will hardly be maintained that even an erroneous explanation is better than none at all.

The upshot of my discussion, therefore, is that we are not yet prepared to frame any adequate general hypothesis as to species formation. The Mendelian-Mutation system of facts and theories appears to me to be no more successful in this respect than its predecessors. In the meantime, let us all busy ourselves with the collection of data of a sort which will be relevant to the final solution. And among these relevant data it is my belief that the facts of geographic variation will bulk as large in the end as those of Mendelian inheritance.

Let us not, however, fall into the error of supposing that the value of every discovery in this field depends solely upon its obvious bearing on the problem of evolution or the mechanism of heredity. If we do this, most of our labors will end in grievous disappointment. It is possible to arrive at results of genuine scientific importance, even if various issues, commonly regarded as fundamental, are for the time being left untouched. Prior to the present studies, no one appears to have taken the trouble even to find out how the geographic races of mammals *seem* to behave in hybridization. Imperfect or superficial knowledge is surely better than none.

THE MITOCHONDRIA PROBLEM

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THE small bacteria-like structures which may be demonstrated in the cytoplasm of all organized cells and which have come to be known as mitochondria have been recognized by biologists although their nature remains obscure. The discovery of these structures may justly be credited to Altmann (1) who believed that they are microorganisms and represent the ultimate units of life embedded in a lifeless cytoplasm of the host cell. Among others, Bütschli and Safftigen upheld a view that these structures are microorganisms having a symbiotic relationship to the host cell. A large number of investigators, however, have assumed a cytoplasmic origin of mitochondria and have preferred to consider them in the rôle of cell organs. That this latter conception has not met with universal acceptance is attested to by the brief consideration that is given to mitochondria in modern textbooks and to the varied opinions that have been advanced by numerous biologists regarding the nature of mitochondria.

In two recent papers (Wallin, 2 and 3), the writer has challenged the validity of the "microchemical" and staining methods that have been used in an attempt to establish a cytoplasmic origin for mitochondria. From the results of the experiments recorded in these papers, together with evidence by analogy therein submitted, the writer concluded that there is more evidence in favor of a microorganismal nature of mitochondria than there has been submitted in the literature to support a cytoplasmic origin of these structures. Since the publication of these papers by the writer, Cowdry and Olitsky

(4) have taken issue with the conclusions arrived at by the writer and assert: "that the discussion provoked may easily lead investigators from the main problem, which is, we take it, the elaboration of new methods for the determination of the chemical constitution of mitochondria as a prerequisite to the study of their rôle in cellular physiology and pathology." The article by Cowdry and Olitsky was followed by an unsigned editorial in the *Journal* of the American Medical Association for November 25, 1922, in which the editor exhibits an apparent unfamiliarity with the evidence in the "controversy."

It is apparent from a perusal of Cowdry and Olitsky's article and the above-mentioned editorial that certain fundamental conceptions must be clarified. These conceptions are primarily concerned with the nature of bacteria. In a previous paper, the writer (Wallin, 2) called attention to the lack of a definition of bacteria. Cowdry and Olitsky offer the following from Park and Williams' textbook on pathogenic microorganisms as a definition for bacteria: "The properties of bacteria . . . which are fairly constant under uniform conditions and which have been more or less used in systems of classification, are those of spore and capsule formation, motility (flagella formation), reactions to staining reagents; relation to temperature, to oxygen and to other food material, and, finally, their relation to fermentation and disease." To which Cowdry and Olitsky add: "the property of forming smaller or larger aggregates (colonies), the individuals of which are, however, physiologically independent (Zinsser), and the development of characteristic modes of growth on suitable artificial media." It is obvious, from the above-quoted statement, that this does not constitute a definition of bacteria nor was it, apparently, so intended by Park and Williams. A definition would include a statement of those properties that are common to *all* bacteria. It would appear unnecessary to emphasize the fact that all

bacteria do not exhibit motility, spore formation and capsules, nevertheless, Cowdry and Olitsky, apparently, assume that *all* bacteria possess *all* the characteristics that Park and Williams include in their system of classification, for, to quote from their recent article: "It must be admitted in all these respects that a great gulf remains between mitochondria and bacteria. In respect to mitochondria definite spores and capsules have not been noted. The mitochondrial blebs which Wallin suggests may be due to fixation bear in our judgment no resemblance to spores. . . . Motility due to flagellar action has not been observed." It appears superfluous to emphasize that biologists in general and bacteriologists in particular have not even assumed that *all* bacteria possess capsules and exhibit motility and spore formation. The absence or presence of these properties serve as a basis for a system of classification of bacteria which in itself implies that these properties are not common to all strains of bacteria. It may appear, in the above quotation, that the writer suggested that mitochondrial blebs may bear a relationship to spores. Such a suggestion was not made by the writer, but to the contrary, he suggested that the mitochondrial blebs described by Cowdry (5) may be due to the action of chemicals just as such bleb-like appearances were produced in bacteria by the action of chemicals (Wallin, 2).

In the absence of a clear and specific definition of bacteria it is important to mention some of the properties of bacteria, particularly those properties that have a bearing on a possible relationship of mitochondria and bacteria. The probable rôle of bacteria in organic evolution has been noted by many biologists and has been clearly indicated particularly by Osborn (6). Their relationship to natural processes in the "economy of nature" is significantly illustrated in the "nitrogen cycle." Space would not permit in this article to give even an abbreviated catalogue of the more important "natural" activities that are due to bacteria. Suffice

to mention such activities as the production of flavor in many of our foods, nitrogen fixation, acetic acid production, etc. The relationship of bacteria to other forms of life is varied and has been investigated chiefly from the standpoint of pathogenicity. It is well known that there are many strains of bacteria which have an intimate relationship to other forms of life, but are not necessarily pathogenic in their reactions. A suggestive and significant example of such a relationship is to be found in the *Bacillus coli* which is nourished by the food in the intestines and in turn renders the food more easily digestible by the host organism (Marshall, 7). It is only recently that this type of relationship of bacteria to higher forms of life has come to occupy the attention of investigators. Aside from a few forms like the root nodule bacteria, the symbiotic bacteria in *Psychotria bacteriophila,* and a few others, very little study has been directed toward the nature of these important life relationships.

The reactions of bacteria to stains and staining methods have also been shown to be quite varied. While the majority of free-living bacteria respond in a fairly uniform manner to the ordinary bacteriological technique, there are many strains which demand a special technique for their demonstration. Apparently, the majority of the strains which require a special technique for their demonstration are those strains that have an intimate relationship with the tissues of higher forms of life.

The cultural properties of bacteria also vary within wide limits. Here again, it appears that those forms which require very special culture media are such strains which have a symbiotic or partial symbiotic relationship to some higher form of life. In some instances an artificial culture medium has not as yet been devised which will encourage the growth of the symbiotic organism. The most significant of such organisms are the microorganisms associated with Rocky Mountain spotted

fever. These organisms, whose pathogenicity and life cycle have been established by Wolbach (8) and a number of co-workers, furnish us with an undisputable example of a known microorganism which exhibits the essential characteristics of mitochondria. Briefly stated, these characteristics are: fragility, as represented by sensitiveness to acetic acid, alcohol, and mechanical manipulation; non-pathogenic in the wood tick and may be transmitted from one generation to another in the egg cell; an intracellular position in the host (apparently, also extracellular); the necessity of a special staining technique that respects their fragility. Concerning these organisms, or more particularly the organisms of typhus fever which have somewhat the same characteristics, Cowdry and Olitsky state: "In pathology these views (*i.e.,* a bacterial conception of mitochondria), if verified, would have a distinct bearing upon our conception of the significance of Rickettsia bodies in typhus fever, trench fever, and other conditions and would leave us in some doubt regarding the criteria to be employed in the identification of microorganisms the nature of which remains obscure." It may be true that a bacterial conception of mitochondria may have a bearing on the ultimate solution of the nature of Rickettsia bodies and it appears to the writer that this is not only possible, but probable. The possibility that the establishment of such a view might "leave us in some doubt regarding the criteria to be employed in the identification of microorganisms the nature of which remains obscure" is far-fetched and is quite irrelevant to the problem as Wolbach (9) has recently called attention to. The known nature, relationships and reactions of Rickettsia bodies leave no basis for any possible confusion with mitochondria, but if there were occasion for the suggested confusion the writer is convinced that *no criterion* is preferable to a *false criterion* in the search for truth.

Cowdry and Olitsky, apparently, demonstrated that

mitochondria are colored in an exceedingly dilute solution (1 : 500,000) of Janus green while some six or eight different strains of bacteria which they subjected to a like dilution of the dye were unstained. Granted that Janus green in a highly diluted solution were a specific stain for mitochondria, would such a staining reaction be convincing evidence against their bacterial nature? On the basis of our knowledge concerning stains and staining reactions in general, the writer is convinced that such evidence is inconclusive. Further, Cowdry and Olitsky failed to stain mitochondria with the Giemsa stain and conclude: "The failure of this so-called nuclear dye to color mitochondria specifically points to a difference which we must consider to be fundamental between mitochondria and bacteria." The writer has definitely stained mitochondria with the Giemsa stain in smear preparations of dog fœtus tissue dried in the air and followed by absolute alcohol fixation.

It is obvious, after a broad survey of the nature of bacterial organisms, that a wide range of variations exists in the bacteria. These variations are concerned with physical and chemical properties and, of greatest significance in a bacterial conception of mitochondria, there are pronounced variations of the relationships of bacteria to other forms of life. This latter variation ranges all the way from a negative, through an indifferent and a partial symbiotic relationship, to a possible absolute symbiosis in which the bacterial symbiont is incapable of development in any natural medium with the exception of a living medium. It is apparent that, if mitochondria are of a bacterial nature, we would not expect them to exhibit the properties of hardy, free-living microorganisms, but rather the properties of such forms that have developed an absolute symbiotic relationship. Again, there are no reasons why one should assume that a bacterial mitochondrium should exhibit pathogenic properties, at least under normal conditions.

It must be borne in mind that only a small fraction of one per cent. of all bacteria are pathogenic. It must, further, be emphasized that some influence in the host cell produces a limitation of growth of the symbiotic organism. Such an influence is, apparently, present in the root nodules of leguminous plants.

The mitochondria problem is primarily concerned with a determination of the nature of these structures and is still an open problem. Further, we believe that the fundamental bearing its solution will have on the future trend of cytological investigation warrants the most thorough and exhaustive researches into the nature of mitochondria. We can not agree with Cowdry and Olitsky that biological investigators may easily be led from the main problem.

LITERATURE CITED.

1. Altmann, R. 1890. Die Elementarorganismen und ihre Beziehungen zu den Zellen. Leipzig.
2. Wallin, Ivan E. 1922. On the Nature of Mitochondria. I. Observations on Mitochondria Staining Methods applied to Bacteria. II. Reactions of Bacteria to Chemical Treatment. *Am. Jour. Anat.*, Vol. 30, No. 2.
3. Wallin, Ivan E. 1922. On the Nature of Mitochondria. III. The Demonstration of Mitochondria by Bacteriological Methods. IV. A Comparative Study of the Morphogenesis of Root-nodule Bacteria and Chloroplasts. *Am. Jour. Anat.*, Vol. 30, No. 4.
4. Cowdry, E. V., and Olitsky, P. K. 1922. Differences between Mitochondria and Bacteria. *J. Exp. Med.*, Vol. 36, No. 5.
5. Cowdry, E. V. 1918. The Mitochondrial Constituents of Protoplasm. Carnegie Inst. Pub., Contr. to Embr., No. 25.
6. Osborn, H. F. 1917. The Origin and Evolution of Life. New York.
7. Marshall, C. E. 1912. Microbiology. Phila.
8. Wolbach, S. B. 1919. Studies on Rocky Mountain Spotted Fever. *Jour. Med. Research*, Vol. XLI.
9. Wolbach, S. B. 1922. Correspondence in *Jour. of A. M. A.*, Vol. 79, No. 24, p. 2022.

THE LIFE HISTORY OF THE FOUR-TOED SALAMANDER[1]

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THE four-toed salamander, *Hemidactylium scutatum* (Schlegel), has long been of interest because of its apparent scarcity and the obscurity of its life history as well as on account of its taxonomic isolation and relationships. It has been found from Massachusetts to Georgia and Arkansas, north through Missouri to northern Michigan, and in more or less of the intervening territory, but it has only rarely been reported as plentiful. The finding of eggs was first reported by Dr. O. P. Hay in 1892 (p. 441), who takes the word of one Mr. Hughes of Indiana to the effect that the eggs as well as the adults were "found in the moss at the roots of trees which stood near ponds." They were neither described nor preserved by the discoverer, however, nor seen by Dr. Hay. They were next found by Mr. S. C. Bishop and Prof. C. R. Crosby near McLean, New York, on May 14, 1919, while sifting for spiders, and later, May 27 and 30, numerous masses of eggs were discovered, with attendant females. These were all found imbedded in sphagnum at the bases of clumps of woody bog shrubs not more than six inches above water. Bishop (1920) followed the development of the eggs to hatching, and to what he considered the beginning of resorption of the gills six days later. Then his last specimens died.

Three years later, May 13, 1922, eggs were discovered near Ann Arbor by the writer in exactly such a situation as described by Dr. Hay thirty years ago. Eggs were found in three widely separated localities (Lima, Iosco, and Whitoak townships) within 12 to 30 miles of Ann Arbor, and at the latter of these places in great abundance. Evidence from these collections and much

[1] Contribution from the Zoological Laboratory of the University of Michigan.

other field work in this vicinity indicates that the eggs of *Hemidactylium* may be expected anywhere in this region where ponds, pools or swamps lie in, or directly adjacent to, deciduous woods, and are so shaded as to support a good growth of mosses or soft rotted wood directly at the water's edge. For it is in such moss, entangled in the rhizoids, or in damp cavities in soft, rotted wood, nearly or quite directly over free water, and from 2½ to 7 inches above the water, that the egg clusters have been found, and almost without exception with an attendant female.

Adult and juvenile four-toed salamanders have been taken by the writer in eight other localities in this region (in the townships of Milford, Scio, Freedom, Pittsfield, Sylvan, Waterloo, Norvell and Hamburg) and in each instance there is a suitable breeding site in the immediate vicinity. Much hunting in many other localities where only one of the two conditions—suitable breeding site and deciduous woods—were present, has so far failed to disclose either young or adults.

The details of breeding behavior and egg deposition have yet to be found out. It may be supposed, however, that fertilization is in some way by means of spermatophores. The adults swim well but only with effort, and cannot live long in water unless there is opportunity for resting at the surface. It is certain, however, that the females take to the water voluntarily, for they were several times found with eggs in clumps of grass and mosses away from shore. The eggs found by Bishop on May 14 were in the neural fold stage, and had probably been deposited about three days. He observed that it took 19 days from that stage to the development of gill and fore limb buds—the condition in which they were first found in Michigan, on May 13th last. Reckoning back 22 days from May 13 gives April 19 as the approximate date of deposition of eggs near Ann Arbor.

Hatching was observed to take place in the field on May 27, but eggs which on May 13 were no further advanced than those left in the field, hatched in the

laboratory four days earlier. It was observed also that eggs kept in water hatched earlier than eggs kept in damp moss. Thus temperature and moisture, and probably other factors, have a direct influence on the period of incubation. But the normal time from egg deposition to hatching figured approximately 38 days. (Bishop found it about 30 in his individuals reared in the laboratory.)

Whether the larvæ of *Hemidactylium* normally enter the water for a portion of their development has never been settled. Evidence bearing directly upon this point is contained in observations on the hatching of a mass of eggs on May 27, 1922. The eggs were at the base of a clump of red-osier dogwood, 2½ inches above water, under a thin moss covering in a few grass roots and some moss rhizoids. An adult female was present. When the female was picked up a larva was sticking to her tail. Two larvæ were noted free from the jelly envelopes, and one had only its head remaining in the jelly. These and several others were found loose in the wet jelly, which may have been partially squeezed by my hand pressing the moss in first opening the nest. One larva was found within 1½ inches of the water, to which a wiggle or two would have brought him. The one with his head caught experienced great difficulty in getting free, but finally did so and then lay for a time in contact with the somewhat sticky mass. Wrigglings at intervals of a few seconds afforded sometimes a little, sometimes no progress, until a stronger wriggle set him free, and he flopped the full three inches into the water below. Two more were watched as they freed themselves head first from their jellies. One made many flops but still stuck by surface tension and the adhesiveness of the jelly, while the wriggles became less frequent. Finally, however, he became free from the jelly and began to make progress downward. In a recess unaltered by my disturbance of the nest, I watched three larvæ wriggle down to the water. Progress was plainly much easier when free from the sticky jelly and from contact with other larvæ. Several others were watched as they emerged from the eggs and

made towards the water. Of the movements that assisted in this progression, some were mere bendings or turnings of the body, others, when horizontal, were like swimming movements, still others were violent wrigglings of the whole body. They appeared to be merely continuations of the movements that all amphibian larvæ make long before free from their jelly envelopes. That these movements led the young four-toed salamanders to their proper environment can scarcely be doubted. Looking down into the water near eggs that had been hatching, I saw one of the newly hatched larvæ above a dead leaf just under the surface of the water. A moment later it had disappeared. With a dip net several larvæ of the same size were taken near the dogwood clump. These larvæ and others secured with a dip net in the same pond at later dates were taken to the laboratory.

To test the theory that the larvæ never enter the water, or do not necessarily enter it, but undergo a short development and transformation in the moss, several dishes were provided with damp moss and eggs nearly ready to hatch, and covered. Controls were kept with free water in the bottoms of the dishes. Lack of time and imperfect technique prevented satisfactory results, but the indications were as follows: (1) larvæ will readily live from 10 to 16 days in no more water than enough to keep their bodies wet, but during this time there is no apparent growth and little if any reduction of the gills; (2) the larvæ do not stay in the moss, but on hatching reach the bottom of the dish and stay there; (3) there is no evident avoidance of a source of light and possibly an attraction toward it. Without doubt much can be learned about the larvæ of *Hemidactylium* from carefully conducted experiments.

A study of development in the laboratory was largely unsuccessful because of the difficulty of providing a constant and sufficient supply of food. The young salamanders were observed to feed readily upon rotifers and entomostracans. When these passed very close to the quiet larva a sudden snap of the head and jaws rarely

failed of a capture. Always, however, the individuals reared in the laboratory were smaller and thinner than those fresh from the ponds. They developed limbs and fingers, it is true, and the limbs came gradually from a merely stick-like supportive function to be used for walking upon the bottom, but normal development undoubtedly depends upon the essentials of a natural environment, *i.e.*, suitable temperature and light, clean pond water, and plenty of small organisms that can be used as food. Furthermore, only one or but very few individuals should be kept in a single aquarium, as when many are kept in close quarters they bite off each other's gills.

MEASUREMENTS IN MILLIMETERS OF JUVENILES OF HEMIDACTYLIUM SCUTATUM.

Larvæ

Time of Collection												
June 11			June 16			June 25			July 2			
Body[1]	Tail[1]	Tail / Body	Body	Tail	Tail / Body	Body	Tail	Tail / Body	Body	Tail	Tail / Body
10.0	8.0	.80	10.0	7.8	.78	10.7	8.3	.77	11.0	6.3	.57
			10.0	7.8	.78	10.9	8.0	.73			
10.0	7.8	.78	11.0	8.1	.74	11.0	8.8	.80			
			11.8	9.6	.81						

Subadults

	Time of Collection								
	July 30			Aug. 20			Nov. 5 and 7		
	Body	Tail	Tail / Body	Body	Tail	Tail / Body	Body	Tail	Tail / Body
	11.5	7.0	.60	11.9	6.9	.58	17.5	16.4	.94
	12.9	9.0	.69	13.7	8.1	.59	18.1	17.2	.95
	13.5	9.2	.68	14.0	9.5	.68	19.0	13.6	.71
	13.8	9.5	.68	14.0	11.2	.80	19.5	17.0	.85
	14.0	11.0	.78	14.0	11.5	.82	19.5	20.8	1.07
				14.9	8.8	.58	20.5	19.1	.93
				14.9	10.9	.73	21.0	19.0	.90
				17.0	15.5	.91	21.3	—	—
Average.....	13.1		.69	14.3		.71	19.6		.91

[1] Body length is measured from tip of snout to just behind the hind leg; the length of the tail is measured from that point to its tip.

Something of development under natural conditions is shown by collections of larvæ in the same pond (Lima township) on June 11, 16, 25, and July 2, and of sub-adults at other places on July 30, Aug. 20, and Nov. 5 and 7.

The specimens collected in June showed only slight differences, but the one taken on July 2, although possessing practically full-sized gills, was distinctly less slender in body and had a noticeably reduced tail. That no collections could be made between July 2 and July 30 is unfortunate, for between these dates the transformation took place. Judging from the state of development of the specimen collected on July 2 and the probable date of drying up of the pond, it may be supposed that transformation took place a little before the middle of July. On July 30 the pond was dry, except for the mud below the superficial dry crust. Search in the moss and grass directly at the edge of the pond revealed five isolated sub-adults, with conspicuously short tails, practically without constrictions, with a black patch on each side of the head showing the position of closure of the gill slits, and with a horizontal black line through the eye (a characteristic of the larva) still conspicuous. On August 20, eight specimens collected under pieces of wood in the shady portion of another dry pond showed increasing size of body, slightly greater proportionate tail length, fainter black gill patches, and, for the most part, faintly indicated caudal constrictions. Those collected in November had longer tails (still much shorter than in adults), no gill patches, well-developed caudal constrictions, but still rather prominent dark postocular lines. Adults, however, often show these lines, although inconspicuously.

These notes are but fragmentary, it is fully realized, but it may be assumed that they prepare the way for a complete life history of this interesting salamander. The story to date may be summarized as follows:

1. The eggs are laid, in the vicinity of Ann Arbor,

about the middle of April or a little later, in clusters imbedded in the rhizoids of moss and roots of grass from 2½ to 7 inches above water.

2. Eggs will not be found unless the breeding site is directly adjacent to a piece of wooded land, nor will adults be found in woods not adjacent to a suitable breeding site.

3. The period from egg deposition to hatching is about five weeks.

4. There is an aquatic larval life of about six weeks.

5. The newly transformed individuals have dark gill patches, a dark line extending from the snout to behind the eye, and disproportionately short tails without basal constrictions.

6. Development during the rest of the season results in obliteration of the dark gill patches, a slight fading of the postocular line, the development of the caudal constrictions characteristic of the adult, and an increase in the proportional length of the tail.

7. The fully adult form and sexual maturity are not attained the first season.

ACKNOWLEDGMENTS

The writer wishes to express his thanks to Miss Doris M. Cochran, of the Division of Reptiles, United States National Museum, for a list of the specimens of *Hemidactylium scutatum* in the collections under her care, and his indebtedness to Dr. Frieda Cobb Blanchard for much assistance in the field work.

REFERENCES

Bishop, S. C.
1920. Notes on the Habits and Development of the Four-toed Salamander, *Hemidactylium scutatum* (Schlegel). New York State Mus. Bull. 219, 220, 15th rep. of director, 1918, pp. 251–282.

Blanchard, F. N.
1922. Discovery of the Eggs of the Four-toed Salamander in Michigan. Occ. Pap. Mus. Zool., Univ. Michigan, No. 126, pp. 1–3.

Hay, O. P.
1892. The Batrachians and Reptiles of the State of Indiana. Rep-State Geol., pp. 412–602.

THE DEVELOPMENT OF ASYMMETRY IN THE FIDDLER CRAB

PROFESSOR T. H. MORGAN

THE experiments of Przibram ('01, '07, '17) and of others have shown in certain species of decapod crustaceans, in which a larger and a smaller "claw" are normally present, that after the removal of the large claw the smaller claw develops into a large claw. In other species, however, including the fiddler crab (*Gelasimus*), this renewal does not take place after the removal of the large claw. A new large claw regenerates on the stump of the old one.

It was known (Hyman, 1920) that in the earliest stages of the fiddler following the Zoea the two claws (first pair of legs) are equal in size and in shape and are like those of the female or like the small claw of the male. I tried to find out whether, if one claw is removed from young male crabs in these undifferentiated stages, the remaining claw will develop into a large claw.

It was necessary first to find at what stage the difference in size of the two claws first appears in the young crabs. Here a new fact of some interest came to light. Collections of young crabs were made at North Falmouth, Massachusetts, on July 10, August 3, September 2 and 15, 1922. Those collected on July 10 were crabs of the preceding summer and will be described later. A new generation came to land in August and September and those of September 2 and 15 give the results shown in the following table. The crabs fall into three groups: (1) those with unequal claws ("male" and "female" claws, or else juvenile, Fig. 1, *c;* and Fig. 2, *b;* and Fig. 3,

FIG. 1. Young crabs 2, 2¼ and 3 mm. across carapace, with narrow abdomens; *a* and *b* have equal small claws; *c*, left claw "large."

a), (2) those with small claws of equal size ("female" or else juvenile, Fig. 1, *a* and *b;* and Fig. 2, *a*), (3) those

FIG. 2. Young crabs (3½ mm.) with narrow abdomens: *a*, has equal small claws; *b* has left claw large.

with two large claws of "male" type (Fig. 3, *b* and *c*, *c'*).

Nine crabs with unequal claws	1	3½	mm. across carapace
	1	3	mm. across carapace
	4	2½	mm. across carapace
	3	2	mm. across carapace
One hundred crabs with equal, small claws .	1	4½	mm. across carapace
	2	4	mm. across carapace
	4	3½	mm. across carapace
	35	3	mm. across carapace
	25	2½	mm. across carapace
	32	2	mm. across carapace
	1	1½[1]	mm. across carapace
Fifty-six crabs with two large claws.	3	4	mm. across carapace
	4	3½	mm. across carapace
	20	3	mm. across carapace
	29	2½	mm. across carapace

It is obvious from this table that a difference in size sufficient to indicate the male type may appear in a few crabs whose carapace measures only 2 to 3 mm. in cross diameter. There were only 9 individuals that showed this male differentiation in the first lot of the table. There were 100 crabs whose carapace measured from 1½ to 4½ mm. with small equal claws. These include all the young female crabs but probably a certain number of males that had not yet shown the male type of claw.

In addition there were 56 crabs whose carapace measured from 2½ to 4 mm. *with two large claws* (male type, Fig. 3, *b* and *c*). These are undoubtedly males that have male claws on both sides. The large number of these crabs seems to indicate that many of the males pass through a symmetrical stage in which both claws have

[1] Below limit of expected change.

the male type. Since such a condition is extraordinarily rare in the adult males—only two cases having been so far recorded—it seems to follow that at a later stage these males must become asymmetrical by the reduction

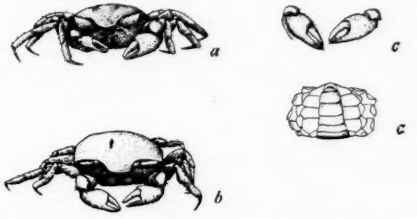

FIG. 3. Crabs (4 mm.); *a* has unequal claws, left large; *b* and *c* have equal large claws; *c'*, abdomen of *c*.

of one of the claws. It was too late in the season to follow up this interesting result, but I hope to study this relation further next summer.

OPERATION ON YOUNG MALES

The first experiments were with the young male crabs collected July 10. The carapace measured from 5 to 7 mm. and the two claws differed not only in size but the large claw had the shape characteristic of the male claw (Fig. 4, *b*). In 56 cases (*A*) the large claw was on the

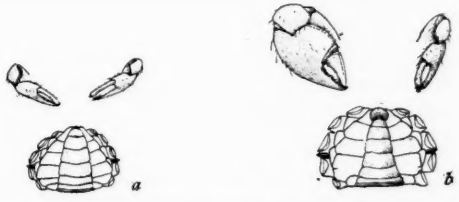

FIG. 4. Female and male crabs (5 mm.); *a*, female with equal claws; *b*, male with right claw large.

left side; in 35 cases (*B*) it was on the right side.

(*A*) After removing the large left claw the crabs were kept until the next molt. Six were lost, six died, the remaining 44 all regenerated a large left claw in place of the large left claw removed.

(*B*) After removing the large right claw all 35 regenerated a large right claw in place of the large right claw removed. It is evident that when the young male crabs have reached a stage in which the two claws have become differentiated, no transfer takes place when the large claw is removed. This is also what happens in the adult crabs.[2]

One claw was removed from young crabs with equal claws that were presumably females (Fig. 4, *a*). In 13 cases (*A*) the left claw was removed; in 17 cases (*B*) the right claw was removed.

(*A*) After the first molt 12 crabs regenerated a new small claw like the one removed. The other claw remained small. In one case a "male" claw developed on the right side. This individual obviously was a male in which the two claws were still equal in size when the operation was carried out. It was the smallest crab present (about 3½ mm.).

(*B*) After the first molt 4 had died, 2 were lost and 10 regenerated a small claw in place of the small claw removed. One regenerated incompletely, but although the left claw was the larger it was not much larger, or in shape like a male claw.

It is clear from these results that if the removal of one claw of the male is to have any influence on the development of the remaining claw it must be removed at an earlier stage, perhaps before the claws have shown a natural difference in size. Operations were then carried out on some of the young crabs collected in August. These were crabs of that year.

Only the smaller crabs were used in which the two claws were seen to be small and alike. The left claw was removed in all cases. The crabs were separated into three lots according to the approximate width of the carapace. As the following table shows, the six smallest crabs were too small to show a differentiation even after

[2] Of 524 adult male fiddlers, 241 had right claw large, and 283 had left claw large.

the next molt but those of the second and third sizes give a positive result.

LEFT CLAW REMOVED	AFTER MOLT
Size 1. (1 to 1½ mm.) 6 crabs.	Both claws small.
Size 2. (2 mm.) 18 crabs	10 had both claws small. 8 had right claw large.
Size 3. (2½ to 3½ mm.) 25 crabs.	12 had both claws small 13 had right claw large.

Of the 18 crabs of the second size (2 mm.) 10 regenerated a small left claw, and in 8 crabs the new right claw was larger and typically male-like.

Of the 25 crabs of the third size (2½ to 3½ mm.) 12 regenerated equal claws after the first molt. Three of these were kept through a second molt. Both claws remained small. The remaining 13 crabs of this third size regenerated a right large claw. Six of these were kept through a second molt and still showed only one (right) large claw.

Since it was not possible to distinguish males from females in these young crabs it is to be expected that about half of the crabs were female, hence for these no enlargement of the new or of the remaining claws is expected. The other half are expected to be male crabs and here a change is possible. It is significant, therefore, to note that about half of the crabs developed a large right claw and none developed a large left claw in place of the one removed. The numbers are regrettably small and there is the further complication that at the stage these crabs have reached after the first molt and perhaps even after two molts there are two large claws even in normal male crabs. It can not be asserted, therefore, that a permanent development of a male claw has taken place as a result of the operation but it seems not improbable that the induced development would lead to the permanent asymmetry of the crab claws.

FURTHER EVIDENCE ON VARIATION IN THE WIDTH OF THE ABDOMEN IN IMMATURE FIDDLER CRABS

PROFESSOR T. H. MORGAN

In an account of some variations in secondary sexual characters of fiddler crabs (The American Naturalist, LIV, 1920) I described and figured several cases in which the abdomens of a few females were narrower than in other individuals of the same size and in this respect might be interpreted either as a variation in the female in the direction of the male type or else as a partial retention of a juvenile condition of the abdomen. After discussing the pros and cons of the situation I concluded that these crabs showed "an apparent change towards maleness or possibly a retention of the juvenile condition." . . . "These questions must be further investigated before a decision can be reached." The following account is a further attempt to discuss the nature of this variation in the width of abdomen of the exceptional cases reported in my former paper. Miss Rathbun (The American Naturalist, LV, '21) criticized my conclusion on the grounds that I offered no evidence to prove that the individuals in question were not simply juvenile stages through which the female fiddler normally passes. Miss Rathbun also stated that verification of her interpretation could be obtained from one of the Californian crabs, *Hemigrapsus nudus*. Fortunately I was able during the winter and spring of 1921 to collect and examine some of these crabs as well as young stages of two other Pacific Coast species. Miss Rathbun also pointed out that in the absence of measurements of the crabs described in my paper and owing to lack of knowledge of the juvenile stages of fiddler crabs it was not possible to determine to what extent the results were exceptional.

As will be shown the stages I described do overlap at one end the juvenile stage, but most of the crabs with narrow abdomens that I referred to occur at a stage when most of the crabs have, as I stated, an abdomen that has its full width. They, therefore, represent, as I supposed, a variation in a secondary sexual character. As the crabs from which the drawings were made are still preserved I can now give their measurements and in addition I can also give the size and condition of the abdomen of fiddler crabs of the same size as well as the relative width of the abdomen both in larger and in smaller crabs.

The fiddlers on which the first part of this paper is based were collected by Miss Phoebe Reed at Pt. Pleasant, N. J., and by Mr. Wm. Procter at Cataumet, Mass. The California crabs were collected by myself from the lower end of San Francisco Bay near Palo Alto, and on the coast north of Half Moon Bay. The measurements have been made by Miss Phoebe Reed, to whose skillful assistance I am greatly indebted. A description of the zoea and megalops stage and of the earliest crab stage that succeed the free swimming stage has recently been given by O. W. Hyman. The oldest stages figured seem to correspond to the youngest stage of my material.

In the earliest crab stage of the fiddler the abdomens of males and females are both narrow and extremely alike. On the innermost surface the rudiments of the appendages are present but it is difficult to distinguish the male from the female condition. It is easier to determine the sex in all except the first two or three stages, by the difference in size of the "claws." This difference is often present in crabs measuring 3 mm. across the thorax. In Table I, crabs having the same width of abdomen are placed in the same vertical column. The width of the carapace of the same crabs is given in the horizontal line. How far the abdomen fails to cover the ventral surface of the crab (*i.e.*, how far it falls short of the bases of the legs) is not apparent from this table and calls for a further statement.

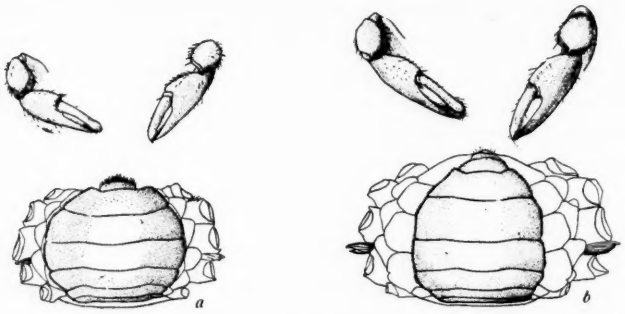

FIG. 1. *a*, female (10 mm.) with abdomen (6 mm.) full width; *b*, female (11 mm.) with abdomen (5½ mm.) less than full width.

TABLE I

Abdomen width mm. \ Carapace width mm.	4	4½	5	5½	6	6½	7	7½	8	8½	9	9½	10	10½	11	11½	12	12½	13	13½	14	14½	15
1		1																					
1½	2	1	3																				
2			6	2	4	1	♂		♂														
2½					1	3	4	2	♂														
3						1	6	9	5	2													
3½								1	9	3													
4									5	4	5	1											
4½										2	6	3	1										
5										1	7	3	1	1									
5½										1	7	6	5	2	1								
6											2	6	21	5	1								
6½													10	10	5	1							
7													13	13	22	7	2	1					
7½													1	5	14	10	6		1				
8															3	12	31	10	5				
8½																4	12	7	2		1		
9																	6	3	15	6	6		

FIDDLER CRABS—♀, *Uca pugnax* (?)

The following partial summary of this table gives the necessary information concerning the condition of the abdomen whether full width or less. Crabs whose breadth was 8½ mm. showed the following conditions. The abdomen of one crab was full width (5½ mm.); in twelve others it was not full size (5 mm., 4½, 4, 3½ and 3).

At 9 mm. two crabs had a full width abdomen (6 mm.); in seven it was 5½ mm., *i.e.,* not quite full breadth; in seven it was 5 mm.; in six it was 4½ mm. (see Fig. 5*A* in earlier paper); and in five it was 4 mm.

At 9½ mm. six crabs out of nineteen had an abdomen 6 mm., *i.e.,* nearly full breadth; in six it was 5½ mm. (see Fig. 5*B* in earlier paper); in three it was 5; in three it was 4½ and in one it was 4 mm.

At 10 mm. the broadest abdomen was full width (7½ mm.); in thirteen it was 7 mm.; in ten it was 6½; in twenty-one it was 6 mm. (like that in Fig. 1, *a;* or Fig. 5*B* in earlier paper); in five it was 5½ mm.; in one it was 5 and in one (2d molt) it was 4½ (one of the variations of earlier paper, *viz.,* Fig. 5*B*).

At 10½ mm. there were five crabs with an abdomen 7½ mm.; thirteen with abdomen 7 mm. (like Fig. 5*B* in earlier paper); ten with 6½ mm.; five with 6 mm.; two with 5½; and one with 5 mm.

At 11 mm. there were three crabs with abdomen 8 mm.; fourteen with 7½ mm.; twenty-two with 7 mm. (two of these had eggs); five with 6½ mm.; one with 6 mm. (like Fig. 5*C* in earlier paper) and in its first skin measured 5½ mm. (Fig. 1, *b*).

In crabs larger than these, relatively less variation was observed and in practically all of them the abdomens would be set down as full breadth, if a little leeway be allowed.

It is evident from the measurements that crabs 8½ to 10½ mm. across the carapace include those stages in which the abdomen becomes as a rule full width. Abdomens of full width may be found in crabs 8½ mm., and this occurs in increasing frequency in the following

"stages" yet in each a few crabs are found whose abdomens are less than full width. It is from the latter group (with one exception) that those figured in my previous paper were taken. It is fairly evident that the condition is due to the failure of the abdomen in some young crabs to attain the full breadth characteristic of the adult females, and in this respect they may be said to retain for a time a more juvenile stage common to both sexes, which stages are more like those of the adult male than like those of the adult female.

How far crabs of a given size represent the same stage in development is not evident from these results. In general successive stages show a measurable size difference, *i.e.*, there is an abrupt increase in size after each molt that comes quickly to an end as the cuticle hardens. On the other hand from the evidence that I have obtained from crabs kept in confinement there may be no increase in size after a molt. Presumably this is due to insufficient food, or to some other condition in the environment. If such conditions occur at times also in nature, then size is not always an accurate measure of age. Whether the abdomen would be more likely to retain its juvenile proportions if the crabs do not grow between molts is not known, but I had already obtained evidence that showed that such a failure does sometimes occur. For example, I kept most of the female crabs with narrow abdomens in dishes of water in the laboratory, feeding them almost daily on as much food (clams and mussels) as they would take. Several were kept till the next molt had occurred, and two, at least, through two molts. In these the abdomen did not increase in width or only slightly so, but these crabs themselves increased in size very slightly or not at all. While I was formerly somewhat more inclined to interpret this result as evidence showing that the variation might be something more definite than retention of the juvenile stage, I am inclined now to think that the evidence is not sufficient to show this, but rather that the result was due

to the failure of the crabs to increase to the normal extent and that the result is correlated with the retention of the more juvenile condition of the abdomen. If, under natural conditions, such influences prevail at times we may find a partial explanation of the retention of the narrow abdomen in crabs of an age (in time) when a full width abdomen is normally attained.

Juvenile Stages of *Hemigrapsus oregonensis*

These crabs (1074 females and 1028 males) were collected in the lower end of San Francisco Bay. Rough measurements made at the time gave the following results. The females measure from 6 to 22 mm. in breadth of carapace and the males from 5 to 25 mm. Amongst the females the smallest crab with abdomen of full width measured about 9 mm. There were seven others in this class with narrower abdomens. Amongst the 10 mm. class, ten had full width abdomens and 23 narrower. Amongst the 12 mm. class, 143 had full width and 16 narrower abdomens. Amongst the 13 mm. class, 244 had full width and 5 narrower (not quite full) abdomens. All others above the last size had full width abdomens.

More accurate measurements of some of these crabs that were made later gave the data in Table II.

The change to full width abdomen took place between 10 and 12 mm. in many of the crabs. There was one 12 mm. with abdomen 9 mm. (full width), two with abdomens not quite full (8½ mm.) and two with distinctly narrower abdomens (6½ and 7 mm.). At 12½ mm. there were 2 with abdomens 9 mm., one crab with nearly full width abdomen (8½ mm.), one with abdomen 7½ and one only 7 mm. The greatest amount of variation in width of abdomen is found in the classes whose carapace measures 9, 9½, 10, 10½ and 11 mm., *i.e.*, at about the time of transformation into the broad type.

It is interesting to note that in one case a crab measuring 8 mm. with a narrow abdomen (4 mm.) carried eggs; five crabs measuring 10 mm. with abdomens 6, 6½,

TABLE II

Carapace width mm / Abdomen width mm.	7	7½	8	8½	9	9½	10	10½	11	11½	12	12½	13	13½	14
3	2														
3½	3	2	1												
4	1		6		1										
4½			3	5	2										
5			1	2	6	2	1								
5½					1	2	3	1							
6					2		1	1	1						
6½					4	2	2	1	2	2	1				
7							3	2	1		1	1			
7½							1		2			1			
8								1	1	2					
8½											2	1			
9											1	2	1		
9½															
10															

SHORE CRABS, *Hemigrapsus oregonensis*, ♀♀

6½, 7 and 7½ mm. also carried eggs; another 10½ mm. (with abdomen 7 mm.) carried eggs; while another 11 mm. (abdomen 7) also carried eggs. The results show that these crabs may become sexually mature before the abdomen has fully attained its characteristic female shape. It may be added that amongst the crabs of these same sizes with abdomens full breadth there were also 23 that carried eggs on the abdomen.

JUVENILE STAGES OF *Hemigrapsus nudus*

The crabs (159 females and 122 males) were collected in the spring of 1921. The females that were measured ranged from 14 to 30 mm. in width of carapace and the males from 9 to 30 mm. Forty female crabs were picked out as showing somewhat narrow abdomens (measuring from 14 to 20 mm.). See Table III.

TABLE III

Carapace width mm. / Abdomen width mm.	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
2															
3		3	1												
4		1	3	6											
5			1	1	5	1									
6						4	3								
7								8	3						
8								2	6	3	1				
9								1	1	10	2	1			
10									1	5	7	2			
11										1	3	3			
12												3	1	2	
13														3	1
14															
15															1
16															

ROCK CRABS, *H. nudus*, ♀♀

The table shows that in the 14, 15, 16, 17 and 18 mm. classes some crabs had abdomens that were full width, while in the same classes there were also crabs whose abdomens were one, two, or three millimeters less than full width. If these millimeter differences in width of carapace correspond even approximately to different molting stages, it appears that some crabs attain the full width of abdomen when they are much smaller than others, or stated conversely, a few crabs do not have full width abdomens, although they are larger than others that have reached this condition.

JUVENILE STAGES OF *Pachygrapsus crassipes*

The crabs (38 females and 40 males) were collected with the last species. The females that were measured

ranged from 14 to 35 mm. in width of carapace and the males from 13 to 40 mm. Table IV gives the measurements.

TABLE IV

Carapace width mm. / Abdomen width mm.	18½	19	19½	20	20½	21	21½	22	22½	23	23½	24	24½
9		1											
9½													
10			1			1							
10½													
11		1	1			1							
11½													
12			2	1									
12½						2							
13										1			
13½						1							
14													
14½										1			
15							1			1		1	

ROCK CRABS RIPPLED, *Pachygrapsus crassipes*

At 19 mm. one crab had abdomen full width (11 mm.). In each of the classes, 19½, 21, 23 mm., there were crabs whose abdomens were full width, but in each there were one or two crabs whose abdomens were one, two, or three mm. less than the former. Above 24 mm. all crabs had abdomens full width.

CONCLUSIONS

Examination of four species of young crabs shows that at first the abdomen is narrow both in the male and female. In the fiddler the abdomen is still narrow in female crabs at a time when the first pair of claws of the male show that secondary sexual differences have already

appeared. Later a certain stage is reached when the abdomen of the young females becomes much wider than that of the male; but not all the crabs of a given size in this period attain the full width of abdomen and in one species a few crabs may even become sexually mature with an abdomen less than full width.

It is clear from the results that at the time when the narrow abdomen of the female changes into a broad abdomen there is much variation as to the extent of the change; and a few individuals with incomplete abdomen may still be found in older stages after the great majority have developed the complete abdomen, characteristic of full-grown females.

SHORTER ARTICLES AND DISCUSSION

GENES FOR THE EXTENSION OF BLACK PIGMENT IN THE CHICKEN[1]

QUITE recently Dunn[2] has reported a dominant autosomal gene which extends black pigment to all or nearly all of the plumage in chickens. This gene he has called "extension of melanic pigment," assigning the symbol E^m. Its recessive allelomorph (e^m) in the homozygous condition is present in the Light Brahma, the Columbian varieties of the several breeds which are like the Light Brahma in color and color distribution, and in the so-called red and buff varieties in which red replaces the white or silver of the Light Brahma.

Certain matings which the writer has made for the purpose of studying the hereditary behavior of other characters tend to confirm his interpretation. A White Plymouth Rock ♂ × Light Brahma ♀ gave an F_1 all of which showed the extension of black pigment throughout the plumage. Differences were noted between the males and females, which, as explained by Dunn, are due to a sex-linked gene which is not concerned in this discussion. With this, as with other crosses to be mentioned, the progeny frequently, indeed usually, showed the presence of genes other than those under discussion, which are incompletely hypostatic to black. In reporting self-blacks and self-blues these are disregarded.

The back crosses, F_1 ♀ × Light Brahma ♀, and F_1 ♂ × White Plymouth Rock ♀, gave only the classes expected on the basis of Dunn's interpretation. The first gave only blacks and the Columbian pattern. The second gave only blacks and whites. In both cases there was a preponderance of blacks, the ratio being, in the first case, 16 blacks to 7 Columbians, and in the second, 31 blacks to 20 whites. In each case equal numbers of the two classes reported were to be expected. The reason for these aberrant ratios is not apparent. In the F_2 the three expected classes

[1] Contribution from the Department of Poultry Husbandry, Kansas Agricultural Experiment Station, No. 20.

[2] Dunn, L. C., 1922, AMER. NAT., 56: 464–466.

appeared though there was quite a deficiency in numbers in the Columbian class. The ratio secured was 25 white, 50 black and 13 Columbian, the theoretical expectation being 22-44-22.

Dunn reported that he had found the gene E^m in White Plymouth Rocks and the classes obtained in the crosses reported above are those expected on the assumption that the White Plymouth Rock, though lacking a dominant autosomal gene necessary for the production of melanic pigment, carries in homozygous condition the gene for its extension (E^m), while the Light Brahma is of the constitution $e^m e^m$ and carries the dominant gene necessary for the production of black pigment, which the White Plymouth Rock lacks.

The writer[3] has reported on a gene for the extension of black pigment in the chicken involved in the hereditary behavior of blue as found in the Andalusian and other breeds. This is also an autosomal gene which has been designated as E. It is a matter of interest to ascertain whether E^m and E are in reality the same gene. The Blue Splashed Andalusian ♂ × Light Brahma ♀ cross, or its reciprocal, should give evidence regarding the situation, as the Light Brahma does not carry E^m and the Blue Splashed Andalusian does not carry E. Such a cross was made by the writer during the past season with the result that of twenty-three chicks hatched all proved to be self-blue.

Mated with this Blue Splashed Andalusian male at the same time were a Buff Orpington, a Rhode Island Red and a Lakenvelder female. The first two show the Columbian pattern with red replacing the white, while the latter is a white bird with black markings similar to, but not identical with, the Light Brahma, probably a modification of the Columbian pattern.

These three females gave only self-blue chicks in the numbers indicated as follows: Buff Orpington—three; Rhode Island Red—ten; and the Lakenvelder—sixteen. The chicks out of the Buff Orpington and Lakenvelder were blue in the down as well as in the adult plumage, while the chicks out of the Rhode Island Red were classified as black in the down, not becoming noticeably blue until nearly grown.

The most reasonable interpretation of these results seems to be that the Light Brahma, Buff Orpington, Rhode Island Red, and presumably the Lakenvelder, which did not carry E^m, did

[3] Lippincott, W. A., 1918, AMER. NAT., 52: 95–115, and 1921, AMER. NAT., 55: 289–327.

carry E, while the Blue Splashed Andalusian carried E^m. This indicates that two separate genes for the extension of black pigment were being dealt with. Since none of the F_1 generation showed the Columbian pattern, the Splashed male must have been homozygous for E^m.

Mated with the Blue Splashed Andalusian male at the same time were females of several other breeds all of which gave self-blue chicks only, in the numbers indicated in the following list, except as noted. The exception is reasonably explained without interfering with the probability that each of these females carried the gene E in the homozygous condition.

Breed	No of Chicks	Color
Silver Spangled Hamburg	7	Self blue
White Cornish	3	Self blue
Brown Leghorn	1	Self blue
Silver Wyandotte	4	Self blue
White Langshan	9	Self blue
White Silky	4	Self blue
White Minorca	14	5 self blue 9 white (blue spots)

The exception to the production of all self-blue chicks came from the White Minorca. This bird was evidently heterozygous for a gene for dominant white. The slight spotting or flecking noted in the white chicks was typical of heterozygous dominant whites and not at all to be confused with blue splashed. The pigmented spots were in every case blue, as was to be expected.

In a former paper [4] evidence was presented indicating that the gene E was carried by White Plymouth Rocks, White Wyandottes and Black Langshans and its presence in White Leghorns was reported as probable. Further matings have shown unmistakably that this gene may be carried by White Leghorns in which the white (assigned the symbol I by Hadley [5]) is dominant. The F_2 generation from a Blue Splashed Andalusian ♂ × White Leghorn ♀ cross contains among other classes self-blues and self-blacks (disregarding the influence of the sex-linked gene for barring carried by the White Leghorn as shown by Hadley [6]), which can be explained only on the assumption that the White Leghorn carried the gene E.

There is evidence, therefore, that this gene (E) is rather

[4] Lippincott, W. A., 1921, AMER. NAT., 55: 289–327.

[5] Hadley, P. B., 1913, Rhode Island Agr. Exp. Sta. Bulletin 155: 151–216.

[6] *Loc. cit.*

widely distributed among breeds of chickens and may be carried by individuals of the White Plymouth Rock; White, and Silver Wyandotte; Black, and White Langshan; Black, White, and Buff Orpington; Light Brahma; Lakenvelder; Silver Spangled Hamburg; White Cornish; Brown, and White Leghorn; White Silky; and White Minorca breeds. It has in fact given no evidence of being in other than the homozygous condition in any individual of these several breeds, which has been mated and which has produced chicks, except certain ones noted in a previous paper [7] that proved to carry R, a gene cooperating with E to produce self-blue and which is either allelomorphic to E, or so closely linked to its recessive allelomorph that it has not been separated experimentally.

There are several genes found in chickens which result in the inhibition of black pigment in certain parts of feathers or regions of the plumage, resulting in the appearance of a more or less definite color pattern. The possibility that the allelomorphs of such genes, whose somatic expression is alternative to self-black, may be necessary to complete the chain of developments and reactions which result in the extension of black pigment to all parts of the plumage even though they are recessive, should not be overlooked. If such a view is ultimately proved tenable, there are not two only, but several genes for the extension of black pigment in the chicken.

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[7] Lippincott, W. A., 1919, *Jour. Heredity*, 10: 7–79.